Monitoring leaf loss and possum impact on New Zealand beech mistletoes

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TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

LIST OF PLATES

ABSTRACT

Numerous anecdotal reports have suggested that possums are the primary cause of mistletoe decline throughout New Zealand, but little quantitative data has been collected to support this claim. The primary goal of this study was to quantitatively assess the annual amount of leaf loss due to possum herbivory, insect herbivory, and leaf abscission on two populations of each of three endemic mistletoe species (*Alepis flavida*, *Peraxilla colensoi*, and *P. tetrapetala*) in four South Island beech forests (Craigieburn, Lake Ohau, Eglinton Valley, and Waipori Gorge). In all six populations, from February 1997 to February 1998, abscission accounted for by far the most leaf loss (range 10-84%, mean 33%), while insects and possums contributed to the mean loss of less than 3% of total leaf area across all six populations. Although possums and insects overall removed similar amounts of plant biomass, possum browse was significantly more heterogeneous than insect browse both on branches within a plant (possum c.v.=2.63, insect c.v.=1.94) and between plants in a population (possum c.v.=2.74, insect c.v.=1.17). Moreover, insects damaged all study plants but removed less than 9% of leaf area per plant, while possums only browsed 32% of the study plants but severely defoliated some plants. Mean leaf loss was significantly greater on plants browsed by possums (62%) than on unbrowsed plants (36%). Thus, while insect damage probably constitutes a predictable stress for most plants, possum browse is unpredictable and may cause a small increase in mortality of affected mistletoes, which could cause a slow decline at the population level for plants with long life-spans and slow reproductive rates.

The second goal of this study was to compare the effectiveness of three commonly used methods of monitoring mistletoes: leaf mapping, visual estimates of plant health (i.e. percent browse scores, foliage density scores, and volume measurements), and photographs. Leaf maps provided the most detailed description of leaf loss but are too laborious to be used on a national scale. Visual estimates were subjective, did not correlate to quantitative leaf map data, and failed to detect the loss of branches. Foliage loss estimated from an examination of repeated photographs corresponded extremely well to leaf loss estimates from leaf maps. A monitoring protocol is suggested that includes photographing mistletoes every winter and visually estimating possum browse each winter and summer.

CHAPTER 1: INTRODUCTION

1.1. IMPORTANCE OF HERBIVORY TO PLANT DEMOGRAPHY AND PERFORMANCE

Both invertebrate and vertebrate herbivores may strongly influence the growth and reproduction of individual plants, as well as population and community dynamics (e.g. Crawley 1989; Lindroth 1989; Weis and Berenbaum 1989; Palmisano and Fox 1997). When herbivory increases plant mortality (of either adults or seeds), population recruitment or adult survivorship may be affected. On the other hand, the predation (especially of seeds) may not have an important population-level effect if recruitment is limited by some other factor, such as the availability of safe sites for seed establishment (Andersen 1989). Characteristics of the plant and herbivore species, environmental factors such as resource availability, and consumption patterns all influence the consequences of herbivory for individual plants and for plant populations (Lindroth 1989; Palmisano and Fox 1997). In addition, the relative effects of insect and vertebrate herbivory on plant performance and demography may shift across environmental gradients, in different habitats, and over time (Hunter and Price 1992; Palmisano and Fox 1997).

Crawley (1989) maintained that vertebrate herbivores generally have greater effects than invertebrates, primarily because mammals are larger and can consume more plant biomass (although lower population densities of vertebrates than invertebrates partially compensate for this). Vertebrates also tend to be more polyphagous, more mobile, and less affected by declines in food quality than invertebrates, all of which may increase their potential effects on plants (Crawley 1989). In addition, higher polyphagy and mobility enables many vertebrates to feed heavily on and thus eliminate "ice cream plants," or species that are so attractive to herbivores that they are eaten whenever they are found (Crawley 1989). On the other hand, the effects of invertebrates may sometimes be cryptic, and only experimentation can reveal the large effects on plant demography (e.g. Waloff and Richards 1977, Kelly 1989).

1.2. Herbivory in New Zealand

Plants have diverse responses to herbivory, including induced chemical defences in leaves (Hodge *et al.* 1998), changes in leaf nutrient concentrations, induced changes in plant morphology, and the stimulation of compensatory growth (Danell *et al.* 1994). Over longer time frames, plants may also develop evolutionary adaptations against damage, such as physical defences (e.g. spines or hairs), toxins (e.g. tannins), and slow growth rates (Coley *et al.* 1985). Because no browsing or grazing mammals occupied New Zealand prior to European settlement, the native New Zealand flora exhibits few of these specialised adaptations that plants on most continents have evolved to cope with mammalian herbivores. Some scientists have suggested that plants in New Zealand evolved certain features in response to browsing by ground-dwelling ratite birds such as the moa (Atkinson and Greenwood 1989). However, introduced mammals browse differently than moas, and thus any adaptations to bird herbivores would not necessarily protect plants against mammals such as possum and deer (Atkinson and Greenwood 1989).

Moreover, other explanations for most of these supposed adaptations appear more parsimonious (e.g. McGlone and Clarkson 1993). For example, Bannister (1989) suggested that crypsis in New Zealand mistletoes could have evolved as a protection against moa herbivory, since cryptic species (e.g. *Korthalsella* spp.) had higher nitrogen concentrations than non-cryptic species (e.g. *Tupeia antartica*, *Ileostylus micranthus*, *Peraxilla* spp.). However, differences in water use and nitrogen uptake may also explain the relationship between nitrogen concentration and crypsis (Bannister 1989), particularly since Australian cryptic mistletoes have the same or lower leaf nitrogen content than their hosts but experience higher herbivory (Canyon and Hill 1997).

Although native plants in New Zealand lack specialised defensive mechanisms against mammals, they do have more generalised anti-herbivore adaptations (e.g. tough, low-nutrient, unpalatable leaves) that may protect them to some degree (McGlone and Clarkson 1993). Still, introduced vertebrates often have dramatic effects on native vegetation, because they are usually polyphagous and unlike insects, they do not develop close associations with one or two plant species (Crawley 1989). (Although introduced insects are often less harmful than introduced mammals, certain generalist

insect species, such as the Asian gypsy moth and the spotted tussock moth have the potential for profound effects on native vegetation). Thus, even if mammalian herbivores had been present in New Zealand for a substantial period, native plant species would probably still have been vulnerable to the introduction of other alien mammal species, as has happened on numerous other continents and islands (Crawley 1989).

A number of mammals have been introduced to New Zealand since the late eighteenth century and have subsequently had a huge impact on native flora in every habitat type (Veblen and Stewart 1982). Dramatic effects have been observed both on individual species (some rare and in danger of local or national extinction, and others that are more common but highly preferred) and on the dynamics of entire ecosystems (e.g. canopy dieback from browsing of dominant species; cessation of forest regeneration in grazed areas). It is increasingly recognised that herbivores have the potential to drastically alter the composition and biodiversity of nearly all native ecosystems, which has led the Department of Conservation to proclaim the reduction of these introduced pests as one of their top conservation priorities (e.g. O'Donnell 1995; Butler 1997). The Australian brushtail possum (*Trichosurus vulpecula* Kerr) is considered one of the most prolific and detrimental pests, and the Department of Conservation now spends approximately $10 million annually on possum trapping and poisoning operations (Parkes *et al.* in press).

There is no doubt that introduced vertebrates have had--and continue to have--extreme impacts on native vegetation. However, in the past it has been difficult to isolate the effects of any single mammal such as the possum, from other confounding factors such as geological changes, disturbance regimes, climate, pathogens, insect herbivory, and the effects of other introduced mammals. Furthermore, detailed ecological data are not available for much of the period of possum colonisation and spread, and thus the claim that possums led to the historical decline of many native species has mainly been supported by anecdotal evidence. Moreover, scientists and managers alike have found it difficult to predict the long-term effects of herbivores such as possums, because no introduced mammal has ever reached an "equilibrium" with native vegetation (i.e. mammals continue to force changes in plant communities by altering the distribution and abundance of certain species and prevent community stability; Cowan 1990a).

1.2.1. The rata example

Meads (1976) conducted one of first detailed studies on the effects of possums on a native plant species. He monitored 24 northern rata trees (*Metrosideros robusta*)* in the Orongorongo Valley, southern North Island between 1969-1974, and he found that although browse varied significantly between trees, three of the plants (12.5%) died because of possum browse during the five-year study. Moreover, seven of 26 additional rata trees in the area also died before 1974, and when possums were excluded from five previously browsed trees, all of the trees recovered. Thus, Meads (1976) concluded that possums were responsible for the decline of rata in the area, and he predicted accelerated mortality as the existing trees died and browsing on the remaining trees intensified.

However, Cowan *et al.* (1997b) reassessed the remaining 21 rata in Meads' (1976) study, and found that none of the trees had died over the ensuing 20 years. Furthermore, 15 of the trees were monitored in detail, and all of them showed nil-to-light browse in 1990. However, between 1990-1994, browse progressively increased, and seven plants showed moderate to heavy possum browse by 1994. Cowan *et al.* (1997b) concluded that possums may severely affect rata health at times, but that the period of high mortality between 1970-74 was probably caused by the confounding effects of possum browse and a severe drought.

This example shows that even studies spanning many years have not always accurately predicted the long-term changes that possum herbivory would cause in plant communities. The rata example also suggests that we should be careful in ascribing plant decline to possum herbivory, because less obvious factors may have confounding effects and alter the consequences of herbivory for plants at different locations and at different times. Various studies have come to quite different conclusions about the overall importance of possum herbivory to native plants compared to other biotic and abiotic factors (e.g. Batcheler 1983, Stewart and Veblen 1983). Such disparities and disagreements have made it difficult for managers to predict the distribution and extent of damage on native flora, and thus, to minimize this damage effectively.

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* Native plant nomenclature follows Allan (1961).

1.2.2. The importance of herbivory to native mistletoes

New Zealand has five extant endemic species of mistletoe in the family Loranthaceae, and all have declined over last 150 years. The reduction in both the size and distribution of populations has primarily been attributed to habitat loss (Norton 1991) and possum herbivory (Ogle and Wilson 1985; Ogle 1997). However, a number of other factors, including fungal disease, insect herbivory, over-collecting, and the loss of native bird pollinators and dispersers may have also contributed to mistletoe decline (de Lange 1997; Ladley *et al.* 1997). Some correlation exists between possum colonisation (or high densities) and the decline of native mistletoes, but vertebrate herbivory alone cannot explain the current distribution and abundance of these plants. Some healthy mistletoe populations persist in areas where possums have been present for some time, and mistletoes on certain islands (e.g. the now extinct *Trilepidia adamsii*) declined in the absence of possums (Ogle 1997). This subject is reviewed in more detail in Chapter 2.

It is probably impossible to unequivocally determine the relative importance of these factors to the historical decline of mistletoes in New Zealand, but their relative importance to the continued survival and reproduction of mistletoes must be understood in order to enable populations to recover and to avoid further decline. Thus, there is a need for more quantitative data on the amount of possum herbivory on mistletoes in different forests, and how this compares to leaf losses due to insect herbivory and abiotic factors such as wind, snow, and natural leaf abscission. These data will also indicate whether the variation in observations of possum browse (and the consequences for plant demography and performance) reflects actual spatial and temporal variability, or whether it is merely an artefact of poorly designed monitoring systems. This may in turn enable managers to more effectively detect changes in mistletoe condition and thus apply the most appropriate management techniques.

1.3. PROJECT GOALS

This study had two primary goals:

1. To quantitatively assess the annual amount of leaf loss due to possum herbivory, insect herbivory, and leaf abscission on populations of three endemic mistletoe species (*Alepis flavida*, *Peraxilla colensoi*, and *P. tetrapetala*) in four South Island beech forests. I was particularly interested in patterns of variation in herbivory over time and

between plant individuals, mistletoe species, and populations from different sites. This study also explores some of the potential sources of this variation (e.g. differences in possums densities and plant palatability).

2. To compare three commonly used methods of monitoring possum browse on mistletoes. The aims were to determine which methodology most accurately estimates leaf damage and to suggest standard monitoring techniques that would allow results to be compared effectively at the national level.

In the following chapter, I give a brief introduction to the organisms (both the endemic mistletoes and the introduced possum) and sites involved in this study. In Chapter 3, I then discuss the current evidence for the effects of possum herbivory on mistletoes, and results from my research are presented in Chapters 4 and 5, which focus on patterns of mistletoe leaf loss. Finally, Chapter 6 focuses on monitoring methods, and Chapter 7 offers some final conclusions and suggestions for future work.

CHAPTER 2: STUDY ORGANISMS AND SITES

2.1. NEW ZEALAND BEECH MISTLETOES

The term 'mistletoe' is used to describe 1400 species of stem hemi-parasites. Their distinguishing characteristic is their ability to sequester water, water-conducted nutrients, and organic solutes through a haustorial intercellular connection to the xylem tissues of the host (Kuijt 1969). In contrast to obligate parasites, they can produce their own food through photosynthesis.

Mistletoes belong to four families in the order Santales: Eremolepidaceae, Misodendraceae, Loranthaceae, and Viscaceae (Cronquist 1981). The first two families are small and confined to the Americas, while the latter two are larger and have a world-wide distribution. Viscaceae contains 400 mistletoe species with small, insect-pollinated flowers, while the Loranthaceae contains 950 species in 50-80 genera, with a primarily Southern Hemisphere distribution (Barlow 1983). Loranthaceae is the most primitive mistletoe family, and most species have hermaphroditic, bird-pollinated flowers.

Nine endemic mistletoe species occur in New Zealand: three species in the genus *Korthalsella* (Viscaceae; Stevenson 1934), and the remaining six species in five primitive relict genera of Loranthaceae. (A tenth species, *Muellerina celastroides*, was recorded last century from the Bay of Islands and is accepted by some authors as native to New Zealand but it is now extinct; de Lange *et al.* 1997a). Ladley (1994) provides detailed descriptions of the evolutionary background, ecology, and reproduction of the Loranthaceae species. *Trilepidia adamsii* was last seen in 1954 and is presumed extinct (Norton 1991). *Tupeia antartica* and *Ileostylus micranthus* have small, insect-pollinated flowers, and they are less host-specific and more common than the remaining three bird-pollinated "beech mistletoe" species: *Alepis flavida*, *Peraxilla colensoi*, and *P. tetrapetala*. These three species were the focus of this study and are described briefly in Table 2.1.

Table 2.1. Characteristics of the three beech mistletoes, *Alepis flavida*, *Peraxilla colensoi*, and *P. tetrapetala*.

	principal host[1]	**maximum plant diameter**[2]	**flowers**[2]	**pollination mechanism**[3]	**fruit**[4]	**current strongholds**[5]
A. flavida	*N. solandri* var *cliffortioides*	1 m	inflorescences of ≤11 yellow flowers; corolla 10-20 mm long	facultatively explosive	yellow; mean diameter = 6.09 mm	mountain beech forests of Canterbury, Otago, & Fiordland
P. colensoi	*N. menziesii*	3 m	inflorescences of ≤10 red/orange flowers; corolla ≤40 mm long	obligately explosive	yellow, egg-shaped; mean diameter = 6.88 mm	Nelson, Haast Valley, western Southland & Fiordland
P. tetrapetala	*N. solandri* var *cliffortioides*	2 m	solitary red flowers; corolla 25-35 mm long	obligately explosive	dull green, urn-shaped; mean diameter = 4.15 mm	mountain beech forests of Southern Alps

[1] de Lange *et al.* (1997b)

[2] Ladley (1994)

[3] Ladley *et al.* (1997)

[4] Ladley and Kelly (1996)

[5] de Lange *et al.* (1997a)

2.1.1. *Alepis flavida*

Alepis flavida has an open, branched architecture, narrow to oblong leaves that are 20-60 mm long, and both secondary runners and haustoria. The small, yellow flowers are facultatively opened by native honeyeaters, although plants can set seed in the absence of pollinators (Ladley *et al.* 1997). Plants are generally at least eight years old at first flowering (Powell and Norton 1994).

The most host-specific mistletoe species in New Zealand, *A. flavida* has been recorded from 13 indigenous host species (de Lange *et al.* 1997b), and more than 80% of herbarium records were taken from its primary host species, mountain beech (*Nothofagus solandri* var *cliffortioides*; Norton 1997). It often co-occurs with *Peraxilla tetrapetala* on mountain beech, where it is usually confined to outer host branches (Powell and Norton 1994; Norton *et al.* 1997). Most *A. flavida* plants grow in the low or middle sections of host trees, and all three of the beech mistletoes usually parasitize large host trees (over 65 cm dbh; Norton *et al.* 1997).

A. flavida has always been sparsely distributed in the North Island, and it is now primarily restricted to the montane areas of the Central Volcanic Plateau and the main axial ranges south of Lake Taupo. In the South Island, plants were once found from D'Urville Island in the Marlborough Sounds south to Waitutu Forest, primarily within high-altitude beech forest (de Lange *et al.* 1997a). Today strongholds include the mountain beech forests of Canterbury, Otago, and Fiordland (de Lange *et al.* 1997a).

2.1.2. *Peraxilla colensoi*

Peraxilla colensoi is the largest mistletoe species in New Zealand, reaching up to 3 m in diameter (Ladley 1994). It has opposite leaves with thick laminae, secondary runners and haustoria, and a complex pollination mechanism that depends on native birds and bees to twist open the explosive flower buds (Ladley and Kelly 1995a, b; Kelly *et al.* 1996)

This species has been recorded on seven indigenous host species and nine exotic hosts (de Lange *et al.* 1997b). Its most common host is silver beech (*Nothofagus menzesii*), and about 80% of its herbarium records were taken from silver beech hosts (Norton

1997). Most plants are found in the middle to upper height ranges of the host tree (Norton *et al.* 1997). *P. colensoi* generally occurs at lower altitudes than *A. flavida* or *P. tetrapetala*, and it occurs most commonly between 1-500 m a.s.l. (de Lange *et al.* 1997a) with an upper limit of 700-1000 m a.s.l. (Wilson 1984; Norton 1997).

P. colensoi has probably always had the most restricted distribution of the beech mistletoes, as it occurs only in silver beech forests of the North and South Islands. This species also appears to prefer beech-broadleaved forest to simple beech or kamahi-beech-rata forest (Norton *et al.* 1997). Historically, *P. colensoi* was uncommon in the North Island, and abundant in only two areas of the South Island: the ranges north of Lewis Pass through to Nelson and the Marlborough Sounds, and from Haast south to Waitutu Forest. Today, it is virtually restricted to these latter two areas (de Lange *et al.* 1997a).

2.1.3. *Peraxilla tetrapetala*

Like its congener *P. colensoi*, *Peraxilla tetrapetala* has opposite leaves with thick laminae, secondary runners and haustoria, and an explosive flower mechanism. Plants are usually at least five years old at first flowering (Powell and Norton 1994). *P. tetrapetala* is less host-specific than the other two beech mistletoes, and it parasitizes 15 indigenous species and two exotic hosts (de Lange *et al.* 1997b). Its most common host is mountain beech (recorded on 60% of herbarium sheets) but north of 38°S, it also commonly parasitizes tawheowheo (*Quintinia serrata*) and in Fiordland it is locally common on silver beech (D. Kelly personal communication). On mountain beech, seedlings often begin growing on outer branches but will only fully develop once secondary runners reach a suitable position close to the main trunk (Powell and Norton 1994; Norton *et al.* 1997). It primarily grows in the low to middle height range of host trees (Norton *et al.* 1997)

P. tetrapetala is the most widely distributed beech mistletoe in New Zealand. Historically, it was uncommon in Northland, but more common south of the Raukumara Ranges, primarily in beech forests of the central and axial ranges (de Lange *et al.* 1997a). Over the past century, it has disappeared from many parts of the North Island, and only a few, scattered populations persist. Its current distribution in the South Island

is similar to *A. flavida*, and the high altitude beech forests of the Southern Alps constitute its main stronghold.

2.1.4. Causes of mistletoe decline

All five endemic mistletoes in family Loranthaceae have declined throughout New Zealand since European settlement around 1840. Decreases in the distribution and abundance of these mistletoes has primarily been attributed to habitat loss (Norton 1991) and possum herbivory (Ogle and Wilson 1985; Ogle 1997). However, a number of other factors may have also contributed to mistletoe decline, including fungal disease, insect herbivory, over-collecting, and the loss of native bird pollinators and dispersers (de Lange 1997; Ladley *et al.* 1997).

The loss of native bird species has probably been particularly important to mistletoes, because mistletoes world-wide are known for their close relationships with bird pollinators and dispersers (Kuijt 1969; McKey 1975; Barlow 1983; Ladley and Kelly 1995a). Native birds, including the tui (*Prosthemadera novaeseelandiae*), bellbird (*Anthornis melanura*), wood pigeon (*Hemiphaga novaeseelandiae*), yellowhead (*Mohoua ochrocephala*), and silvereye (*Zosterops lateralis*) ingest and disperse mistletoe fruits (O'Donnell and Dilks 1994; Ladley and Kelly 1996). Ladley and Kelly (1996) showed that germination is entirely dependent on bird dispersal (to ensure removal of the fruit exocarp), which is almost solely accomplished by native avian species (especially tuis, bellbirds, and silvereyes). Thus, limited dispersal may constitute a limit to population densities, although probably only after a substantial time period.

Declining numbers of bird pollinators may pose a more immediate threat to the beech mistletoes, since all three species have a complex pollination mechanism. Native birds and bees (introduced species are ineffective pollinators) twist open the explosive, ripe flower buds to obtain a substantial nectar reward (Ladley and Kelly 1995; Kelly *et al.* 1996). *Alepis flavida* is in the least danger of pollination failure, because flowers are facultatively explosive and can self-open, and plants are highly self-fertile and have high seed set rates even in the absence of pollinators (Ladley *et al.* 1997). Therefore, for this species, low pollinator visitation would probably result in lower rates of outcrossing, rather than overall depressed reproductive output. In contrast, *Peraxilla*

flowers are obligately explosive, and unopened flowers are significantly less likely to set seed (Ladley *et al.* 1997). Therefore, the reduction of native pollinators such as tui and bellbirds could have resulted in inadequate pollination, which may have contributed to the rapid decline of mistletoe populations over the past 50 years.

2.2. AUSTRALIAN BRUSHTAIL POSSUM (*TRICHOSURUS VULPECULA* KERR)

2.2.1. General characteristics

The common brushtail possum (*Trichosurus vulpecula*) is the most widespread of the three possum species native to Australia. Two distinct colour forms, grey and black, have been introduced to New Zealand: 'blacks' predominate on the West Coast of the South Island and in native forest, while 'greys' are more common on farmland and in drier, open country (Cowan 1990a).

A typical adult possum weighs between 1.4- 6.4 kg, with little differentiation between the sexes (Green and Coleman 1984). Possums on average are larger in the South Island (mean 3.04 ± 0.08 kg) compared to the North Island (mean 2.45 ± 0.04 kg; Cowan 1990a). Male possums mature at 1-2 years old, while females may breed in certain environments by 9 months. Most births occur in autumn, with an occasional second, smaller pulse in spring, depending on female condition. Young become independent about eight months after birth. Thus, populations are usually largest between February and May (after an influx of newly independent young) and lowest between September and October (because of winter mortality; Brockie *et al.* 1981).

Possums are largely arboreal but spend 10-15% of their time on the ground (Cowan 1990a). They possess a prehensile tail and sharp claws that enable them to jump from branch to branch or scale up tree trunks. They are also capable of swimming but generally avoid water. As nocturnal animals, they generally emerge from dens about 30 minutes after sunset and return several hours before dawn (Winter 1976). Feeding generally occupies 1-2 hours each night, starting two hours after sunset, and possums typically feed at 2-4 different sites during the night (Winter 1976; MacLennan 1984).

During the day, the animals remain in dens, which are usually located above the ground in hollow trees, clumps of vines or epiphytes, or ceiling cavities of buildings. However,

possums are not limited by the availability of elevated dens, as they can also exploit clumps of flax, blackberry, gorse, fallen logs, haystacks or woodpiles, or the burrows of other animals (Cowan 1990a). In some areas, 60-70% of nest sites are at ground level (Kerle 1984).

The home range of males is generally significantly larger (mean 1.9 ha) than for females (mean 1.3 ha; Green 1984). Movements of up to 30 km have been recorded (Clout and Efford 1984), and possums may move particularly long distances through forest to forage in pasture (Green and Coleman 1981). Clout and Gaze (1984) found that even within continuous forest, adults frequently moved at least 1 km during an evening. This high mobility and the ability to disperse facilitates rapid reinvasion of an area after control operations (Clout and Gaze 1984; Cowan *et al.* 1997a). Females usually remain at their natal base while juvenile males disperse, and thus, colonising populations are often characterised by an excess of males (Green and Coleman 1984; Cowan *et al.* 1997a), while stable populations usually have an equal sex ratio or female bias (Crawley 1973; Green 1984).

2.2.2. Possum diet

Possums are opportunistic herbivores, feeding mainly on leaves, but also ingesting buds, flowers, fruit, bark, fungi and invertebrates. They have also recently been found to eat significant quantities of eggs, chicks, and adult birds (Innes 1995). A wide range of native tree species, ferns, and vines and epiphytes have been recorded in their diet (Green 1984), as well as cultivated grains and vegetables, ornamental shrubs and flowers, and small birds and mice (Cowan 1990a). Pasture grasses may also constitute a significant food source for possums denning up to 1 km from the forest edge (Coleman *et al.* 1985). Possums ingest the fruits of 65 native plant species, generally in proportion to their availability in the forest (Coleman *et al.* 1985; Cowan 1990b). Buds and flowers are also commonly eaten and may comprise up to 40% of possum diet during some seasons (Fitzgerald 1976; Kerle 1984; Owen and Norton 1995). Invertebrates may also constitute a significant source of protein; although most studies suggest they contribute only a small amount of biomass (e.g. Cowan and Moeed 1987), Owen and Norton (1995) found that invertebrate larvae contributed up to 28% of the diet during the winter.

Possums generally exhibit pronounced preferences for some plants relative to their availability. Fuchsia (*Fuchsia exorticata*), rata (*Metrosideros robusta* and *M. umbellata*), kamahi (*Weinmannia racemosa*), five-finger (*Pseudopanax arboreus*), mahoe (*Melicytus ramiflorus*), kohekohe (*Dysoxylum spectabile*), wineberry (*Aristotelia serrata*), titoki (*Alectryon excelsus*), and toro (*Myrsine salicina*) are all heavily browsed wherever they occur (Fitzgerald 1981). At any given location, the possum diet primarily consists of only a few species, even in diverse forests (e.g. Fitzgerald 1978; Coleman *et al.* 1985; Allen *et al.* 1997), but the relative preferences among these browsed species vary between regions for unknown reasons (e.g. Mason 1958; Fitzgerald 1976; Leathwick *et al.* 1983; Coleman *et al.* 1985). In addition, possums alter food choices seasonally (Fitzgerald 1978; Owen and Norton 1995), and they maintain strong preferences for certain individuals of a species (e.g. Meads 1976; Owen 1993). This selectivity led Nugent (1995, p. 7) to suggest that "although the population as a whole might be able to withstand possum browsing if it were evenly spread across all species, depletion continues because individuals within species are selectively targeted."

Possum preferences may be related to numerous factors including: the local abundance and distribution of available food sources (plant species, fruit, invertebrates, etc.); variation in plant architecture; variation in leaf toxins and/or nutrients (Fitzgerald 1978; Kerle 1984); attributes of the possums themselves (e.g. sex; behavioural characteristics); or environmental variables such as season, rainfall and altitude (Coleman *et al.* 1985). Furthermore, possums are easily able to switch to other food items once their preferred sources are depleted (Kerle 1984).

2.2.3. Possum colonisation and spread in New Zealand

Possums were first introduced to New Zealand from Australia in the mid-nineteenth century to establish a fur trade. The first successful liberation was accomplished near Riverton, Southland between 1837 and 1840, and most importations were made by regional Acclimatisation Societies, especially between 1890-1900 (Pracy 1974). Additional liberations of New Zealand-bred progeny accelerated the dispersal of possums throughout the country between 1890-1940.

Initially, it appeared that possums were creating a valuable industry, and during the 1890's, the government actually limited trapping to prevent possum extinction. Orchardists first complained about possum damage in 1910, but reports from Australia attested that possums only caused minimal damage in their native habitat. Not until 1919 did anyone question the effects on native species, but Kirk (1920) clearly declared that "the damage to New Zealand forests is negligible and is far outweighed by the advantage that already accrues to the community."

Despite Kirk's comments, evidence for the detrimental effects of possums accumulated after 1922, and the government refused applications for further liberations between 1920-1940. However, they still expected that commercial harvesting would limit populations sufficiently (Pracy 1974), and there was little concern for the effects on native forests. Cockayne (1928) suggested that "if damage of any kind there be, it is so slight as to be negligible...At any rate, if it is proved eventually, which is most unlikely, that opossums are a menace to forests, their skins are so valuable that at any time the animals can be reduced in numbers to the extent desired without any cost."

In the early 1930's, V. D. Zotov noted damage to native forests by possums, but he did not publish his results until 1949 (Zotov 1949), and by this time, public opinion had swung against the protection of possums. In 1947, the government recognised the need to limit possum populations; all restrictions against trapping were dropped, penalties for liberations were increased, and poisoning was legalised. Illegal liberations continued through the 1950's, but the detrimental effects of possums on native species and especially on cattle (as a vector for bovine tuberculosis) have been increasingly recognised. Approximately $10 million is now spent annually to alleviate the effects of possums on native species across a 13,000 km^2 area (Parkes *et al.* in press).

2.2.4. Current distribution and abundance in New Zealand

Possums are now abundant throughout the North Island, except on the northern slopes of Mt. Taranaki, Mt. Ruapehu, and in the northern Auckland province (Pracy 1980). They are also widespread in the South Island, except in parts of South Westland and western Fiordland and in the upper catchments of a few rivers in South Canterbury and northwest Otago (Pracy 1980). Possums continue to disperse into these areas, and may soon inhabit most of these regions. They were also introduced to 17 offshore islands,

13 of which they still inhabit, including Stewart Island and the main Chatham Island. They have been successfully eradicated from D'Urville Island, Kapiti Island and Codfish Island (Cowan 1990a).

Possums can tolerate diverse habitats, including all types of indigenous forest from sea level to bushline, montane scrub and tussock grasslands, introduced and native grasslands, exotic forests, shelter belts, orchards, swamp and pakihi, sand dunes, and urban areas (Cowan 1990a). Forests are their primary habitat, and densities reach their maximum in hardwood forests and along forest/pasture margins (Coleman *et al.* 1980). Measured possum densities in various habitats are presented in Table 2.2.

Table 2.2. Possum densities recorded from different habitat types in New Zealand.

Habitat	**Estimated possum density (possums per hectare)**	**Source**
podocarp-broadleaf forest	10-12	(Coleman *et al.* 1980; Brockie 1982)
pine plantations	1-3	(Warburton 1977)
scrubby farmland	1	(Jolly 1976; Triggs 1982)
beech forest	0.5	(Clout and Gaze 1984)

Densities tend to decrease with increasing altitude, but this trend is probably a function of vegetation changes rather than a direct response to environmental gradients (Coleman *et al.* 1980; Clout and Gaze 1984). Possums can endure rainfalls of 350-8000 mm per year and altitudes up to 2400 m, often ranging above the snow line (Cowan 1990a). Environmental conditions have only prevented their colonisation in the extremely wet, mountainous areas of western Fiordland or where large rivers have excluded them.

2.2.5. Effects of possums on native flora

Possums have adapted well to new diets and habitats in New Zealand, and they generally have fewer parasites, predators, and competitors than in their native Australia. Their high fecundity, the early dispersal of young, and their ability to exploit a wide range of plant species have enabled them to reach up to 20 times their average densities in Australia (Kerle 1984; Cowan 1990a). Consequently, although possums cause only minor damage in Australia (mostly in plantations and farms), they affect the New Zealand environment to a much greater extent. They lead to economic losses in exotic

plantations, catchment plantings, and on farms and stations, and they have affected native species in diverse natural habitats.

Canopy defoliation and mortality may occur when possums heavily browse forests dominated by a few preferred species, such as the podocarp-broadleaf forests of the southern North Island and Westland (Coleman *et al.* 1980; Batcheler 1983; Pekelharing and Reynolds 1983; Green 1984; Leutert 1988). The overall importance of possum browse versus natural stand dieback (Veblen and Stewart 1982; Stewart and Veblen 1983), climatic effects (Grant 1985, 1989), and the confounding effects of other animals such as deer and goats (Fitzgerald 1981) has generated vigorous debate. However, it is now generally agreed that catastrophic dieback is typically caused by possums when populations reach peak levels (approximately 15-25 years after colonisation; Batcheler and Cowan 1988; Rose *et al.* 1992), although susceptibility to dieback may also depend on stand history, age, and diversity, substrate type, and landform (Stewart and Veblen 1982; Payton 1983, 1988; Reif and Allen 1988). Canopies that are weakened by browsing may then be more susceptible to windthrow, climatic extremes, and insect or fungal outbreaks (Green 1984; Cowan *et al.* 1997b. Browse may also increase canopy gaps, which alters the influx of light into the forest interior and selects for light-demanding understory plant species (Fitzgerald 1976; Brockie 1992).

In more diverse forests, the selective browsing of preferred plant species may cause gradual changes in forest composition (Fitzgerald 1978; Campbell 1990). For example, in the Orongorongo Valley, two non-palatable species (*Elaeocarpus dentatus* and *Laurelia novae-zelandiae*) have increased in abundance, while the two main species in the possum diet (*Metrosideros robusta* and *Weinmannia racemosa*) have decreased in abundance (Allen *et al.* 1997). Moreover, these induced changes in vegetation do not appear to affect possum densities greatly, because possums can easily switch to other food sources once their preferred foods are depleted (Green 1984).

Possum control has been emphasised in broadleaf forests, especially those dominated by rata or kamahi, because canopy dieback or major compositional changes are most likely to occur in these habitats. In contrast, the role of possums in beech forests has been largely overlooked, both because possum densities are relatively low and because the dominant species, *Nothofagus* spp., is rarely browsed (Wardle 1984). However, as early as 1956, Grant suggested that montane beech forests may be susceptible to browse, and

James (1974) pointed out that seral vegetation along stream channels and on mass movement sites would be particularly vulnerable.

Moreover, less palatable biomass is available to possums in beech forests, and thus, despite low possum densities, the browsing pressure on preferred species is similar to other forest types (Owen 1993). For example, Owen and Norton (1995) found that the four main plant species in the possum diet comprised only 5% of total foliage biomass in the beech forest at Haast. Thus, although possums probably pose no risk of canopy collapse in beech forests, possums still have important implications for the forest composition and biodiversity (Rose *et al.* 1993; Pekelharing *et al.* 1998a). In particular, there is a need to focus on species, such as mistletoes, that are rare and might be driven to local or national extinction by possums (Nugent 1995).

2.3. STUDY SITES

2.3.1. Site descriptions

This study was conducted in four beech (*Nothofagus* spp.) forest sites spread across the South Island (Figure 2.1). Table 2.3 briefly describes the physical characteristics and locations of these sites, and more detailed descriptions of the four areas follow. These sites were chosen because they support apparently healthy, large, dense populations of beech mistletoe with a sufficient number of accessible plants to perform this experiment. No significant possum damage had been observed on the Craigieburn and Lake Ohau mistletoe populations over the previous four years (J.J. Ladley and D. Kelly personal communication), while the Eglinton and Waipori populations had been seriously attacked by possums in the past (C. Rance personal communication and personal observations).

Figure 2.1. The location of the six mistletoe study populations. The three species (*A. flavida*, *P. colensoi*, and *P. tetrapetala* were each studied at two beech forest sites in the South Island.

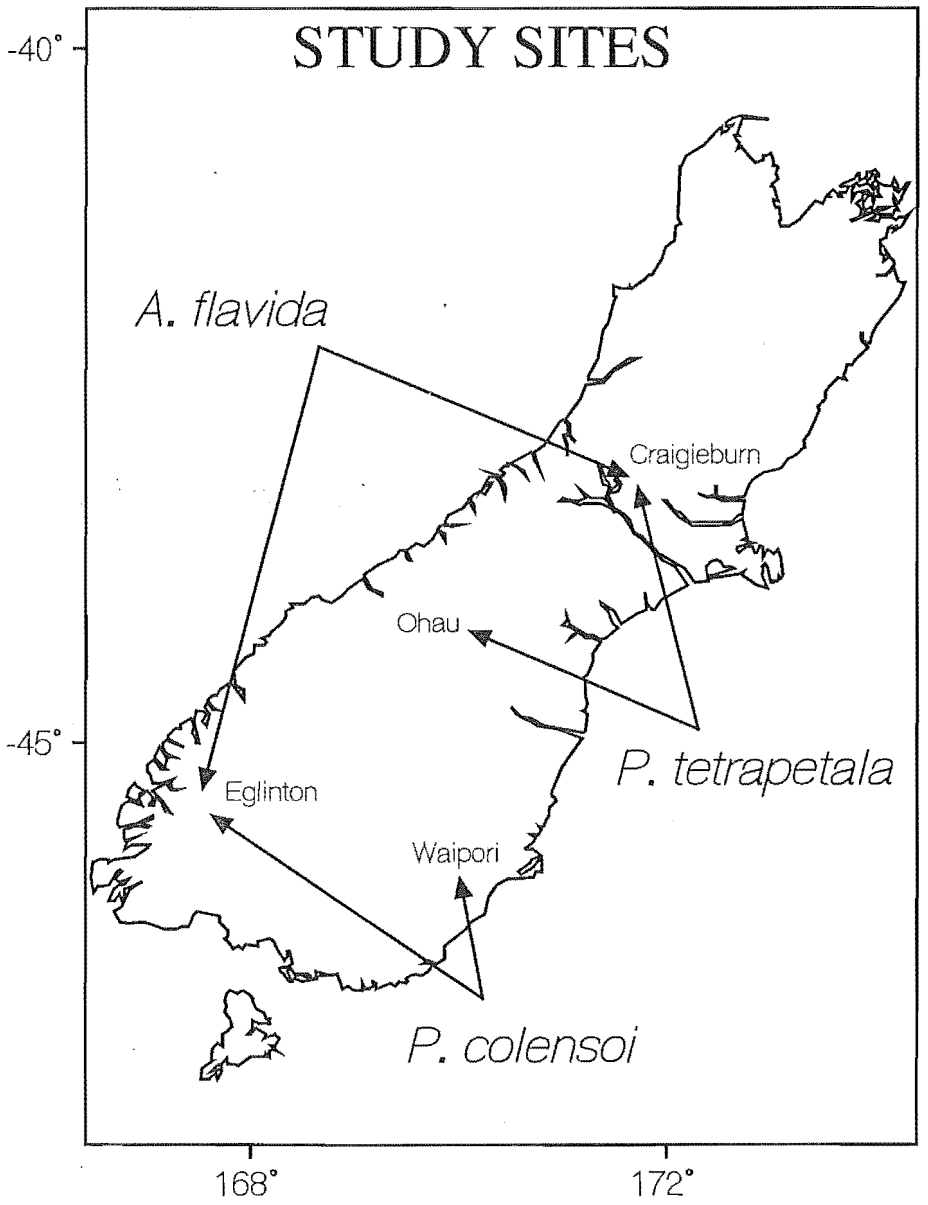


Table 2.3. Location and descriptions of the four study sites.

Site name	Grid reference (NZMS 260 map series)	Latitude, Longitude	Altitude	Annual rainfall	Mistletoe and host species present
Craigieburn	K34 050831	43°09'S 171°43'E	940 m	1400-2000 mm	*P. tetrapetala*, *A. flavida* on *N. solandri*
Lake Ohau	H38 557618	44°12'S 169°49'E	540 m	1200-4800 mm	*P. tetrapetala*, *A. flavida* on *N. solandri*
Eglinton Valley	D41 166727, D41 172708, D41 164668, D42 154582	44°58'S 168°01'E	350-380 m	2300 mm	*P. colensoi*, *P. tetrapetala*, *A. flavida* on *N. menziesii*
Waipori Gorge	H44 794716, H44 799715	45°55'S 170°2'E	40 m	500-1200 mm	*P. colensoi* on *N. menziesii*

2.3.1.1. Craigieburn

The Craigieburn study site is located in Craigieburn State Forest Park, Canterbury, approximately 100 km west of Christchurch and 80 km from the West Coast. The 20 mistletoes used in this study (10 *A. flavida* and 10 *P. tetrapetala*) were distributed throughout the forest near Jacks Pass (Figure 2.2).

The Craigieburn Range forms part of the watershed between the Waimakariri and Rakaia catchments. The underlying bedrock is primarily steeply tilted and faulted greywacke and argillite of the Triassic/Jurassic age with small amounts of interbedded volcanic rocks and cherts (Shanks *et al.* 1990). The study site is surrounded by steep mountains formed through glaciation and periglacial activity and altered by post-glacial erosion. The soils are highly erodable high-country yellow brown earths of the Kaikoura set with approximately 10-15 cm of topsoil (Ledgard and Baker 1988).

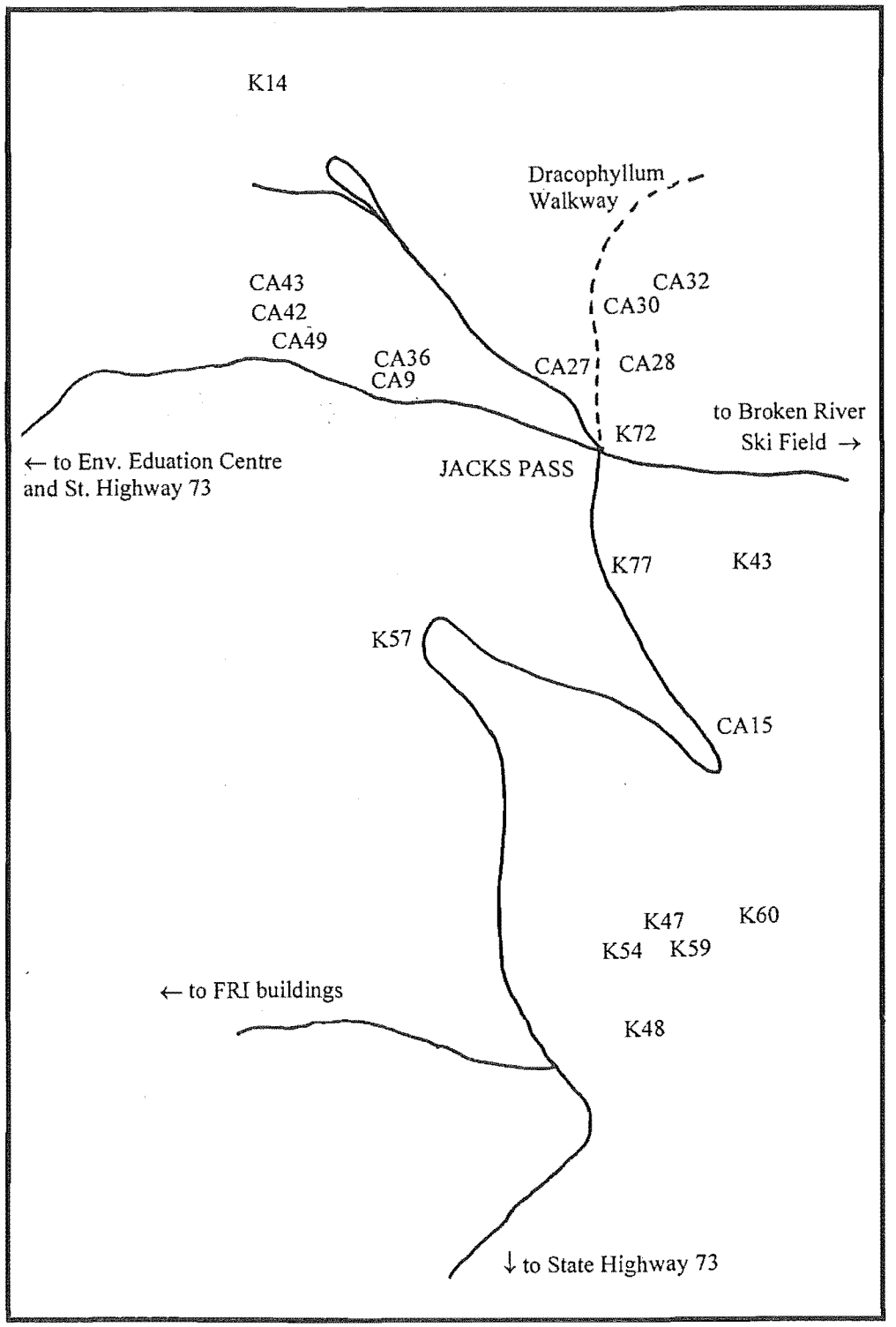
Annual mean rainfall at Craigieburn is between 1400-2000 mm, and snow is common at higher altitudes and may occur during any month (Ledgard and Baker 1988; Shanks *et al.* 1990). Average temperatures vary between 13.9°C in February to 2.0°C in July, but unseasonable temperature fluctuations are common (Ledgard and Baker 1988). The frequent strong, gusty winds from the Northwest often cause drought conditions during the summer months.

The Craigieburn forest is dominated by mountain beech (*Nothofagus solandri* var *cliffortioides*), and the forest consists of a mosaic of patches of various ages, the oldest trees being 260 years old (Ledgard and Baker 1988). *Peraxilla tetrapetala* and *Alepis flavida* grow commonly throughout the area on *N. solandri*. The understory is open and consists of a small number of vascular species, most commonly mountain toatoa (*Phyllocladus alpinus*) and *Coprosma parviflora*. A number of ferns and bryophytes also inhabit the understory.

There are also several small areas of grassland dominated by browntop (*Agrostis tenuis*) and fescue *(Festuca novae-zelandiae*) with scattered areas of scrub (Ledgard and Baker 1988). A number of exotic species have been planted in the area since 1954, including *Eucalyptus* spp., willow (*Salix* spp.), birch (*Betula* spp.), alder (*Alnus* spp.), and most

notably, a sizeable experimental plot of *Pinus* spp., which has spread across the adjacent Helicopter Hill.

Figure 2.2. Location of the 10 *A. flavida* (marked 'CA') and 10 *P. tetrapetala* (marked 'K') study plants in Craigieburn State Forest Park.



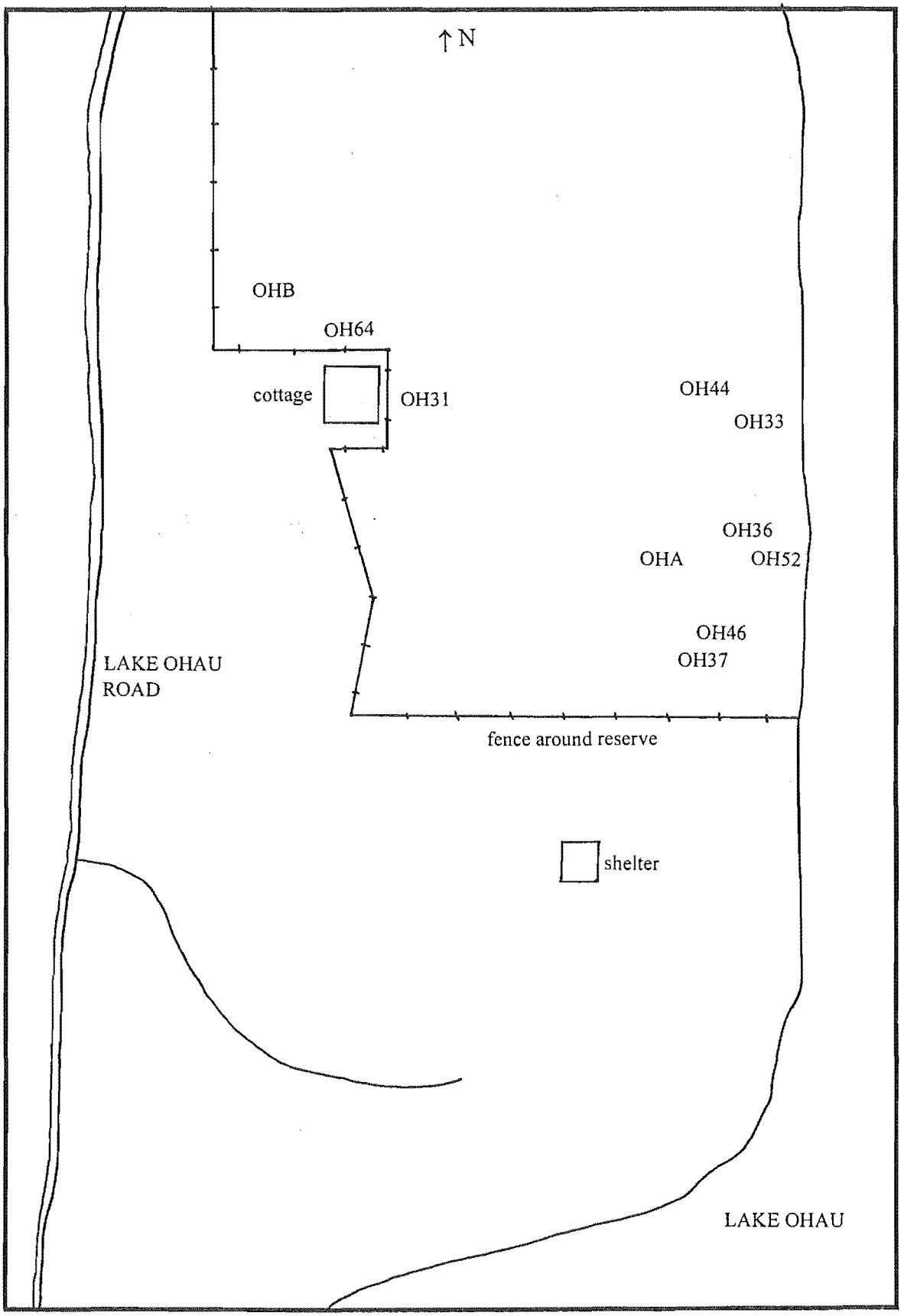
2.3.1.2. Lake Ohau

The Lake Ohau study site was located in Round Bush Reserve, a 12.14 hectare forest remnant reserve on the western shore of Lake Ohau, Central Otago. The 10 *P. tetrapetala* plants used in the study were located along the lake edge of the reserve and in the interior of the forest fragment (Figure 2.3).

Lake Ohau, the only large lake in the Mackenzie Basin that has not been raised for hydroelectricity, is a moraine-dammed glacial lake located in a broad valley of greywacke and argillite and surrounded by schist mountains. The soils are hydrous high country yellow-brown earths that are moderately fertile but droughty in the summer (McEwen 1987). The area has a humid, inland climate with cold winters and warm to cool summers. Annual rainfall varies widely between 1200-4800 mm, and the prevailing North-westerly winds are frequently strong and gusty (McEwen 1987). The eastern edge of Round Bush reserve is particularly susceptible to the drying and damaging effects of the frequent winds across Lake Ohau.

The western edge of Lake Ohau is primarily grassland that is grazed by cattle and sheep with interspersed areas of scrub, comprised mostly of matagouri (*Discaria toumatou*), sweet briar (*Rosa rubiginosa*) and *Coprosma* spp. Isolated clumps of Hall's totara (*Podocarpus hallii*) and mountain toatoa (*Phyllocladus alpinus*) occur close to the valley floor. Small remnants of manuka (*Leptospermum scoparium*) and mountain beech forest are also scattered through the grassland matrix, primarily around small riverbeds. Round Bush is dominated by mountain beech with very few other species in either the canopy or the understory. Cattle were free to graze in the reserve until 1989 when a fence was placed around the forest remnant. However, cattle still often get into the reserve, and understory growth is still extremely limited.

Figure 2.3. Location of the 10 *P. tetrapetala* study plants in Round Bush Reserve, Lake Ohau.



2.3.1.3. Eglinton Valley

The Eglinton Valley runs North-Northeast to South-Southwest within Fiordland National Park. It is a large, glaciated valley with steep sides and a flat floor 0.5-1 kilometre wide. The underlying bedrock is primarily composed of metamorphic and igneous intrusive rocks covered by alluvial soils on the river flats and strongly leached to podzolised soils in other areas (McEwen 1987). Rainfall can exceed 2300 mm annually, and mean temperatures range between 0-8°C (Elliott 1996).

The valley is mostly forested up to 1000 m a.s.l. apart from some large open, grassy areas on the outwash fans. The forest is dominated by red and silver beech on the valley floor, with mountain beech increasingly common at higher altitudes. Under the canopy, the forest is open with a few understory plants and a ground cover of mosses. The most common understory plants are mountain toatoa (*Phyllocladus alpinus*) and broadleaf (*Griselinia littoralis*; O'Donnell 1996).

The 20 mistletoes used in the study were located at four sub-sites in the mid-section of the valley (Figure 2.4):

1. **Totara Flat**: Five *Alepis flavida* were studied in an isolated mountain beech stand surrounded by grazed grassland between the Eglinton River and State Highway 94. Five additional *A. flavida* were located along the edge of continuous forest on the eastern side of the Highway (Figure 2.5.a). The forest is dominated by mountain beech with occasional red beech (*Nothofagus fusca*), and a narrow band of pasture separates the forest and the road. This area is located the farthest away from the other sub-sites and supports the only known substantial mistletoe population in the central Eglinton Valley outside of the possum control operation (Rance and Rance 1995). Possum control was initiated in the area in November 1998, partly because of the rapid decline in the condition of *Alepis flavida* over the previous year.
2. **Deer Flat**: Three *P. colensoi* were studied in an isolated stand of mountain beech on a morainic knob adjacent to the Eglinton River, approximately 66 km from Te Anau and one kilometre south of Knobs Flat (Figure 2.5.b). The forest is dominated by silver beech with some red and occasional mountain beech. This sub-site, as well as Knobs Flat and Dore Pass, are located within a possum control area of 6400 hectares. A reassessment in June-July 1998 showed a 2.14% residual catch rate

prior to further control and a 0.56% residual catch rate after five weeks of control (trapping and 585 feratox bait stations).

3. **Knobs Flat**: One *P. colensoi* was located approximately 200 m east of the old NZDA hut (Figure 2.5.c). The forest has a discontinuous canopy and is composed primarily of silver beech with some red and occasional mountain beech.
4. **Dore Pass track**: Six *P. colensoi* were located in scattered silver beech trees along the true left of the Eglinton River on the Dore Pass track, approximately 400 m from the carpark (Figure 2.5.d). The isolated trees are surrounded by grazed pasture.

Figure 2.4. Location of the four study sub-sites in the central Eglinton Valley, Fiordland National Park.

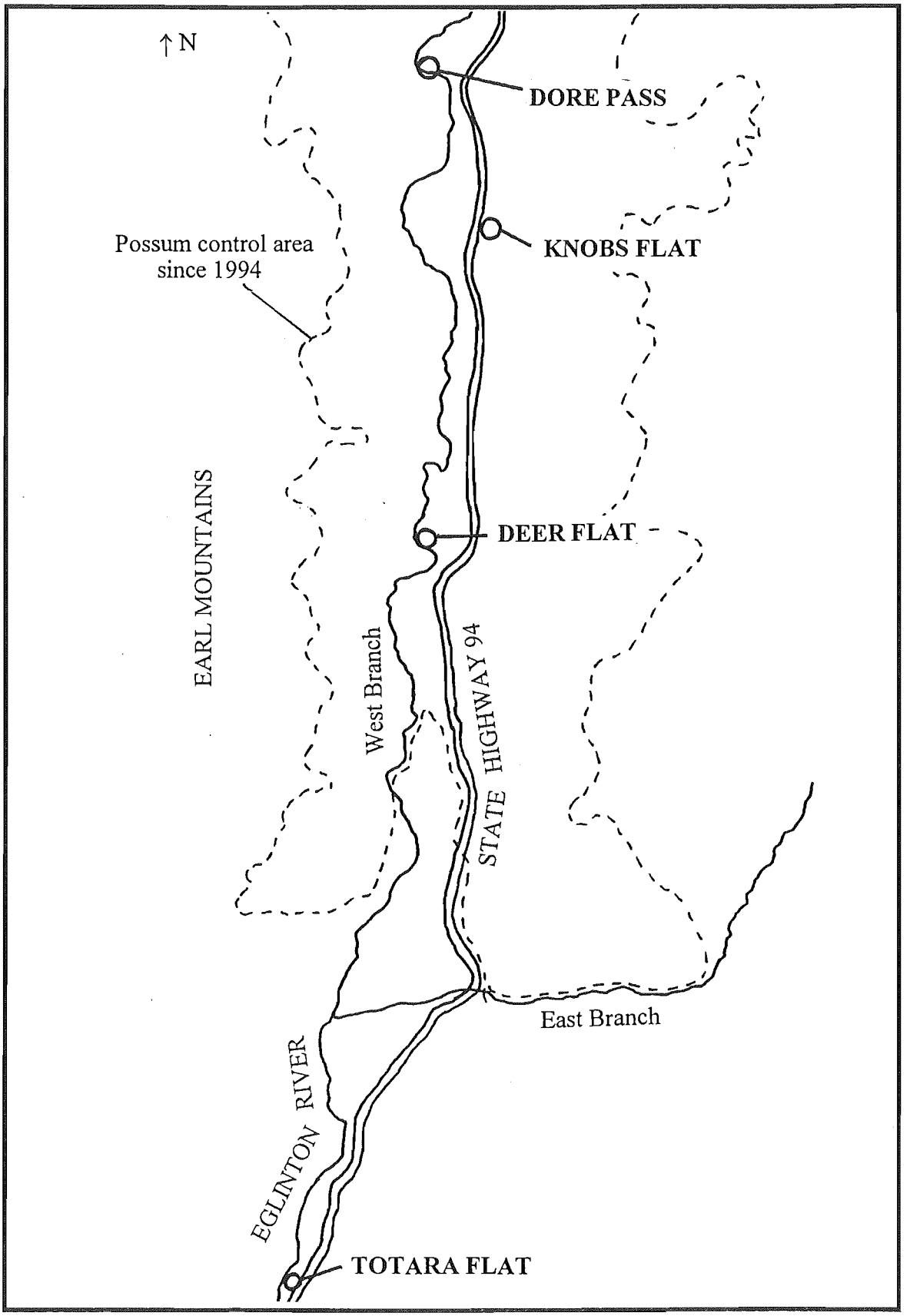
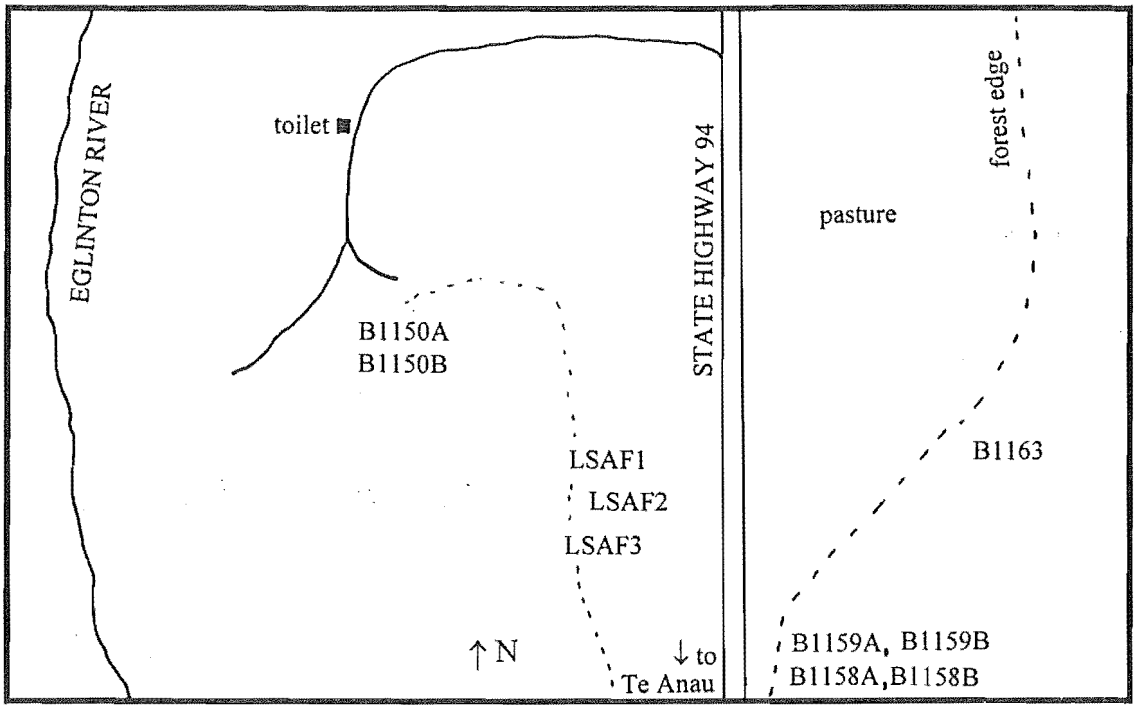
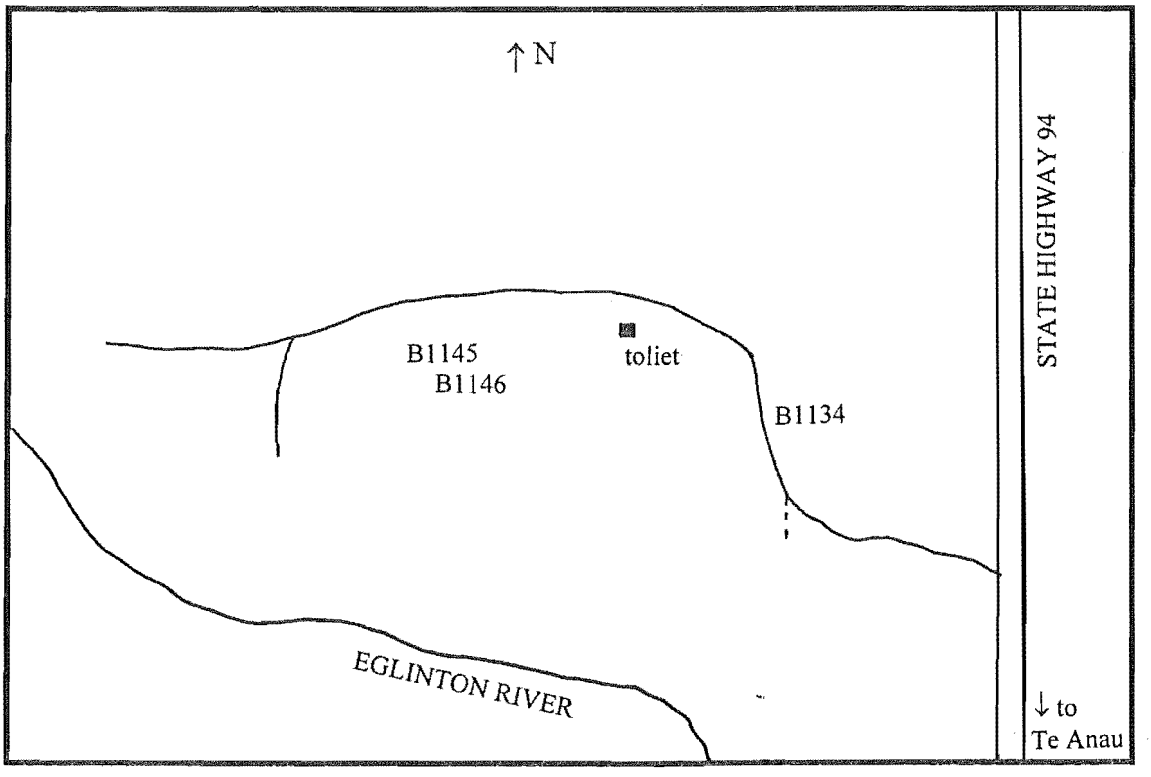


Figure 2.5. Location of the Eglinton study plants at the four sub-sites: **(a)** the 10 *A. flavida* plants at Totara Flat, **(b)** the three *P. colensoi* at Deer Flat, **(c)** the one *P. colensoi* at Knobs Flat, and **(d)** the six *P. colensoi* at Dore Pass.

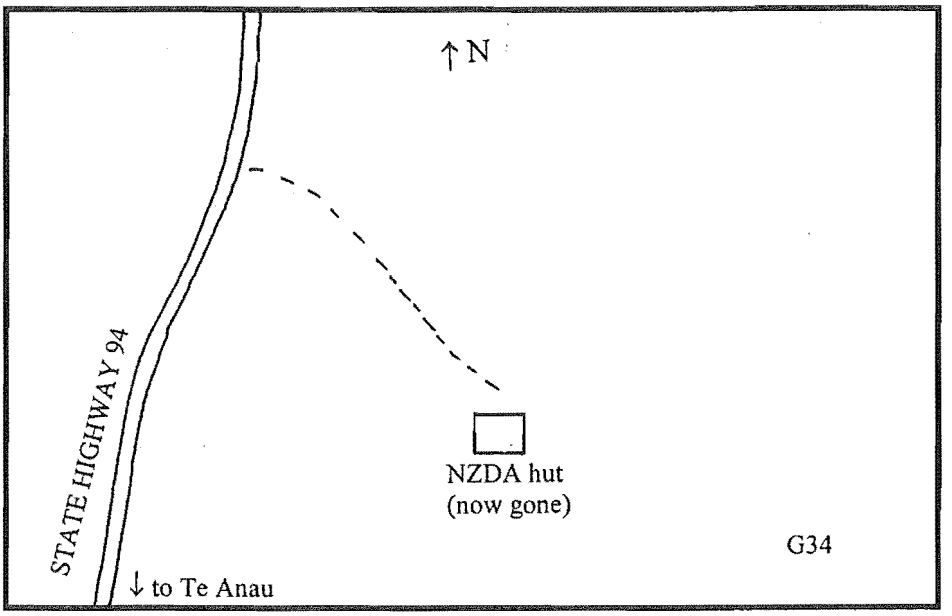
a) TOTARA FLAT



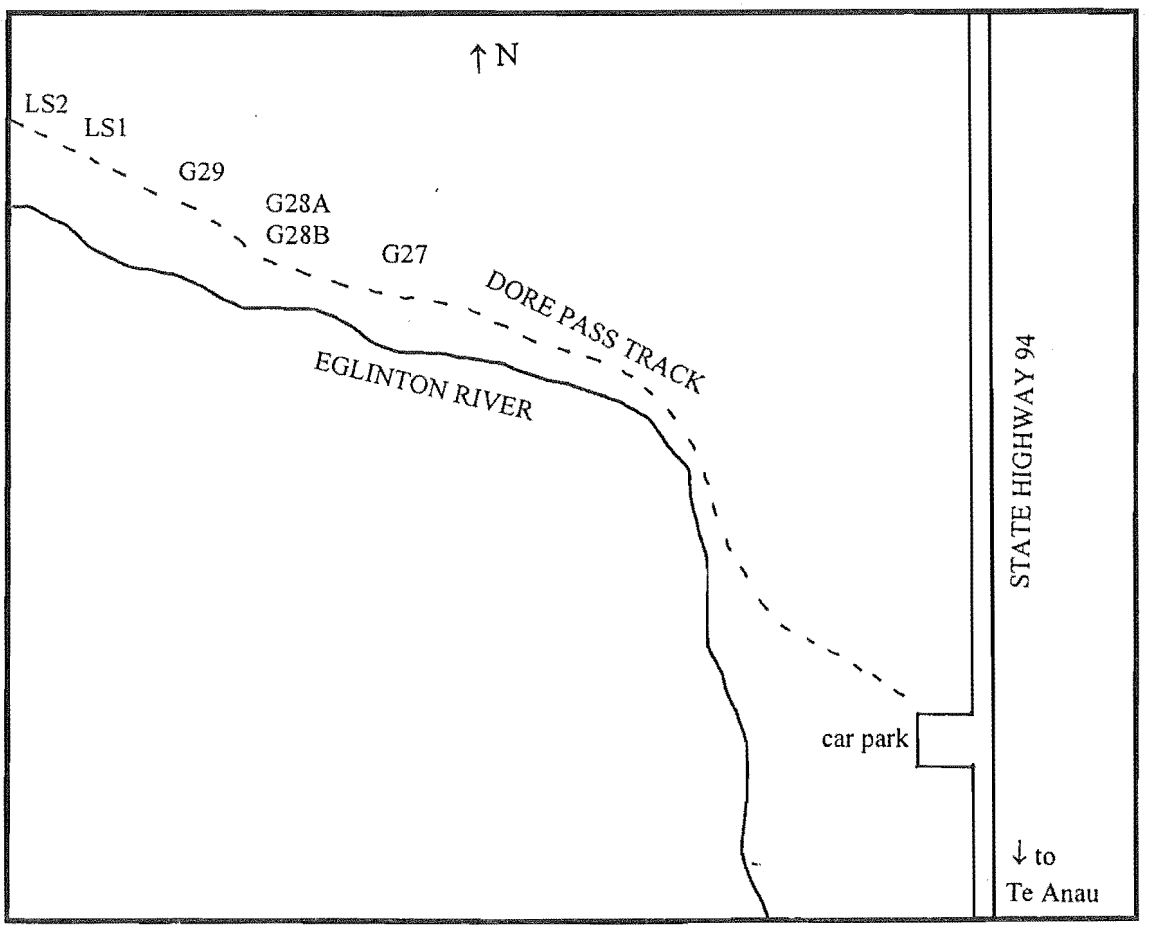
b) DEER FLAT



c) KNOBS FLAT



d) DORE PASS



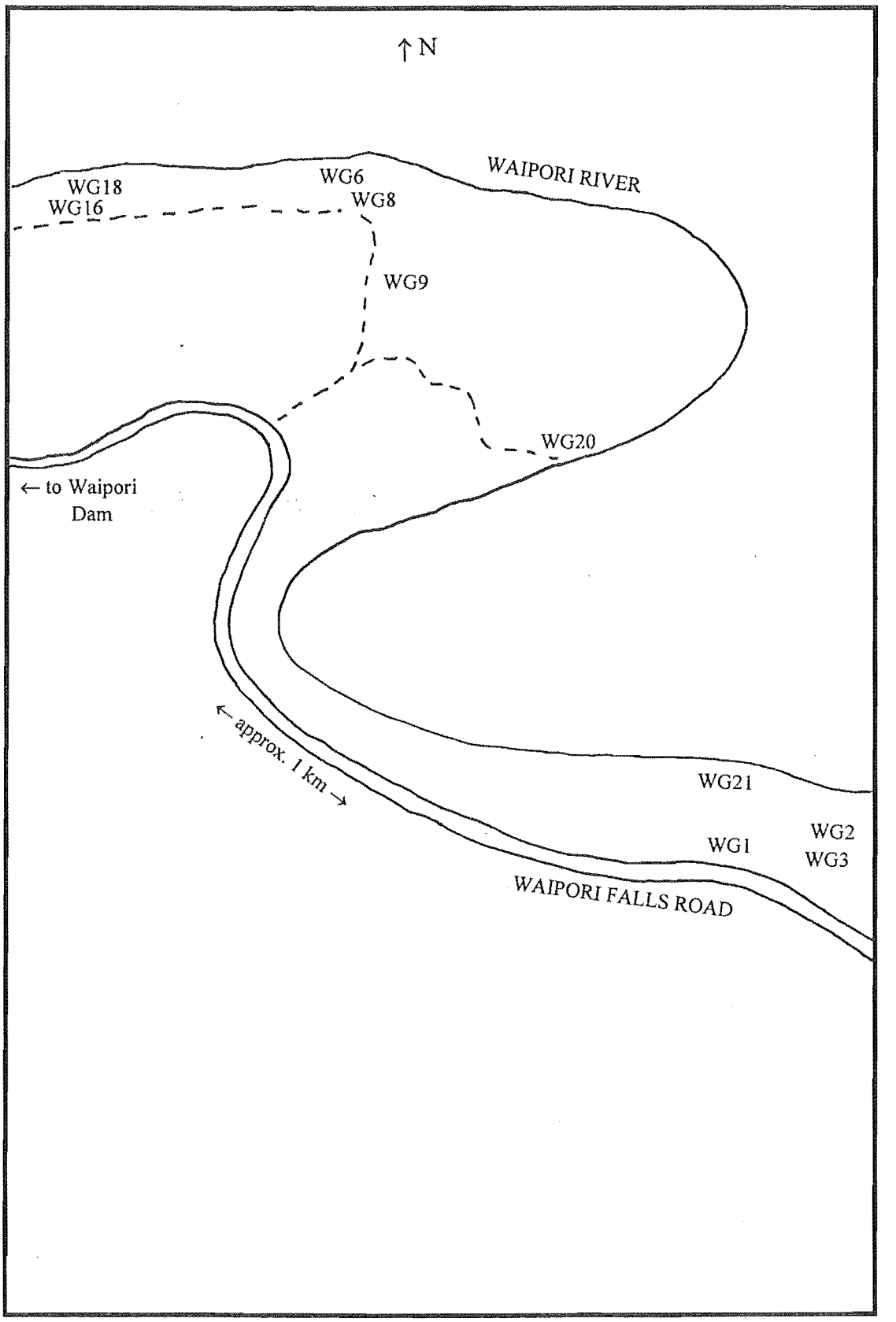
2.3.1.4. Waipori Gorge

The Waipori Gorge site is located between the Waipori Falls Road and the Waipori River, downstream of the Wapori Falls Dam. Six *P. colensoi* were studied in silver beech trees along the river and surrounded by a large area of grazed pasture, and four additional *P. colensoi* were located approximately 1 km to the east in essentially continuous silver beech forest (except for the intervening road; Figure 2.6).

Waipori experiences a cool, moist climate with an annual rainfall of 500-1200 mm. The prevailing winds are from the Northwest. The bedrock is mostly Paleozoic-Mesozoic schists, and soils range from deep to shallow because of the variable cover of loess or drift (McEwen 1987). Throughout the Waipori Ecological District, a few small relict stands of silver beech and podocarp-hardwood forest persist in a grassland matrix. Patches of manuka and kanuka forest and scrub are also scattered through the region.

The study plants were located in forest remnants dominated by silver beech with an open understory. Common plants in the understory include broadleaf (*Griselinia littoralis*) and *Coprosma* spp. The pasture is dominated by exotic grasses such as browntop (*Agrostis tenuis*).

Figure 2.6. Location of the ten *P. colensoi* study plants at Waipori Gorge. Plants were located at two sub-sites approximately 1 km apart.



2.3.2. Possum densities

Mistletoes are still locally abundant at all four study sites, and thus possums do not appear to have affected these populations to the degree that mistletoes have been harmed in other areas (e.g. North Island, Mt. Misery). However, decline potentially could have occurred in the Eglinton Valley without the recent possum control operation, and regional variations in browse were apparent at the beginning of this study. Since 1995, very little possum browse had been observed on *Peraxilla tetrapetala* at Lake Ohau, and it appeared uncommon on *P. tetrapetala* and *Alepis flavida* at Craigieburn since 1992 (J.J. Ladley and D. Kelly personal communication). In contrast, *P. colensoi* at Eglinton was heavily browsed prior to the initiation of a local possum control operation in 1994, and *A. flavida* at Eglinton occurred outside the control area and was still being browsed at the commencement of this study (C. Rance personal communication). Similarly, possums had severely browsed *P. colensoi* plants at Waipori prior to December 1996, leaving at least four plants dead and several others heavily defoliated.

The most obvious explanation for this site-to-site variation is simply that the latter two sites support higher possum densities than the former two locations. This explanation seems especially plausible given the higher plant diversity in the forests at Waipori and Eglinton than in the relatively homogeneous forests of Craigieburn and Lake Ohau. Thus, at the conclusion of the mistletoe monitoring study (February 1998), I conducted trap-catch experiments at Craigieburn and Ohau to estimate the relative possum densities at these sites. The Department of Conservation conducted a similar study in February 1998 at Waipori Gorge. Unfortunately, no pre-control density estimates were available for the Eglinton Valley, and possums are now maintained at low densities (less than 5% residual trap-catch rate) around all four Eglinton sub-sites.

2.3.2.1. Methods

Trapping at Craigieburn and Ohau followed the Department of Conservation's standard trap-catch methodology (Warburton 1997), so that these results would be directly comparable to results from Waipori and from other Department of Conservation trapping programmes. At Craigieburn, seven trap-lines were placed at approximately

200 m intervals across the study area. All but one of the lines were located entirely within beech forest; four of these lines ran primarily through dense regrowth, while two lines were mostly within more open, mature forest. The final line was placed between Cave Stream and the Broken River ski field access road, where small patches of beech trees are surrounded by grasses and exotic vegetation.

Five lines were placed at 200 m intervals in and around Round Bush Reserve, Ohau at right angles from the lake shore. Three of the lines began in the beech forest within the Reserve and extended into areas of manuka, kanuka, and scrub. The remaining two lines were placed 200 m and 400 m south of the Reserve through areas of matagouri, manuka, and scrub.

Each line began from a randomly selected starting point and followed a compass bearing to avoid concentrating sampling in easily accessible areas. The lines consisted of 10 traps spaced at 20 m intervals, with the first trap 20 m from the starting point. Victor No. 1 traps were secured with chains and metal staples to the closest tree (or other secure object), and baited with a 5:1 mixture of flour and icing sugar. Miller (1993) showed that leg-hold traps were three times as efficient and considerably more humane than Timms traps. Traps were set for three consecutive fine nights (12-14 March 1998 at Craigieburn and 19-21 March at Ohau), and each day all the traps were cleaned (e.g. any fur removed), reset, and replenished with lure. All trapped possums were killed; weighed, measured, and sexed; and then disposed of according to DoC regulations.

Trap-catch rates (mean possums captured per trap night) were calculated by: 1) counting the total number of possums captured plus identified possum escapes (trap sprung with possum fur inside); and then 2) dividing this number by the number of trap-nights (number of traps multiplied by number of nights, minus one-half of a trap-night for each non-target catch or sprung-and-empty trap).

2.3.2.2. Results

Tables 2.4 and 2.5 show the number of possum and non-target species caught on each line at Craigieburn and Lake Ohau. Summary details are reported in Table 2.6. In 210 trap nights at Craigieburn, there were 34 possums caught, seven identified possum

escapes, two non-target catches (one ferret and one stoat), and five sprung-and-empty traps. The most possums per trap-night (0.38) were caught on Line 1, which ran through dense, regenerating beech. The lowest catch rates were on Lines 5 and 6, which ran through mature beech forest. The trapped possums weighed between 1.3-4.0 kg, and an even number of males and females were captured (the age and sex of two possums were not recorded). The total mean possums caught per trap-night at Craigieburn was 19.85%.

In 150 trap-nights at Ohau, I recorded ten possums trapped, three identified possum escapes, six non-target catches (three hedgehogs and three ferrets), and two sprung-and-empty traps. Possum catches were evenly distributed across all five lines. The trapped possums weighed between 2.1-4.7 kg, and more females than males were caught (the sex and weight of three possums were not recorded). The total mean possums caught per trap-night at Ohau was 8.90% (Table 2.5).

Table 2.4. Trap-line summaries from Craigieburn, 12-14 March 1998.

line number	trap-nights set	possum catches	possum escapes	non-target catches	sprung/ empty	mean possums per trap-night
1	30	10	1	0	2	0.3793
2	30	6	2	0	0	0.2667
3	30	6	0	0	0	0.2000
4	30	5	1	1	0	0.2034
5	30	2	0	1	1	0.0690
6	30	0	2	0	2	0.0690
7	30	5	1	0	0	0.2000
TOTAL	210	34	7	2	5	0.1985

Table 2.5. Trap-line data from Lake Ohau, 19-21 March 1998.

line number	trap-nights set	possum catches	possum escapes	non-target catches	sprung/ empty	mean possums per trap-night
1	30	2	0	4	0	0.2799
2	30	2	2	1	2	0.1404
3	30	2	0	0	0	0.0667
4	30	3	0	0	0	0.1000
5	30	1	1	1	0	0.0678
TOTAL	150	10	3	6	2	0.0890

Table 2.6. Summary data from possum trapping at Craigieburn and Ohau in March 1998.

	Craigieburn	Ohau
total trap nights*	206.5	146
total possum catch**	41	13
immature catch***	6(M), 4(F)	1(M), 2(F)
adult catch***	10(M), 12(F)	1(M), 3(F)
mean possum weight***	2.62 kg	3.09 kg
mean possums per trap-night	0.1985	0.0890

*one-half trap night subtracted for each non-target catch or sprung-and-empty trap
**including possum escapes
***sex, age, and weight not recorded for two possums caught at Craigieburn and three caught at Round Bush

2.3.2.3. Conclusions

Trap-catch data is a useful measure of the relative differences in possum densities between sites, provided a standard methodology is utilised for the comparisons. Table 2.7 shows trap-catch rates from Ohau and Craigieburn compared to rates calculated by the Department of Conservation at Waipori Gorge, the South Branch of the Hurunui River Valley, and the western slopes of the St. Arnaud Range at the head of Lake Rotoiti, Nelson Lakes. Possum densities in the Hurunui and Lake Rotoiti are much lower than densities at my three study sites, even though mistletoes at Hurunui and

Rotoiti appear to be damaged more by possums than at my study sites (Wilson 1984; Grant *et al.* 1998; see also sections 3.1 and 3.3.2).

Table 2.7. Trap-catch rates for four beech forest sites.

Site (date)	**Trap-catch rate (possums per 100 trap-nights)**
Craigieburn (March 1998)	19.85
Ohau (March 1998)	8.90
Waipori (March 1998)	19.53*
Hurunui (February 1996, February 1997)	3.73- 4.54**
Lake Rotoiti (September 1997)	6.5- 8***

*rate for all 15 DoC lines across the entire area; the rate on the three lines closest to my study plants was 14.29%
**pre-poisoning rates from treatment and non-treatment areas; see Grant *et al.* (1998)
***pre-poisoning rates from treatment and non-treatment areas; see Pryde (in prep.)

Pekelharing *et al.* (1998b) found that the degree of defoliation of fuchsia (*Fuchsia excorticata*) was significantly related to local possum density in South Westland. In contrast, the above results suggest that mistletoe condition does not vary predictably according to possum density. The trap-catch rate at Ohau was double the Hurunui rate, yet very little browse has been observed on *P. tetrapetala* at Ohau since 1995 (J.J. Ladley unpublished data; personal observation). The trap-catch rates at Craigieburn and Waipori were both more than five times the Hurunui catch, although possum effects at both sites were low, and such rates are considered high for beech forest (Butler 1997). The high catch rate at Craigieburn is particularly surprising, because of the high density of *Peraxilla tetrapetala* and *Alepis flavida* in the area. Moreover, the equal sex ratio and abundance of adults caught at Craigieburn indicates that this possum population is stable rather than colonising (Green and Coleman 1984; Cowan *et al.* 1997a).

Because pre-control data was not collected in the Eglinton Valley, the possibility that a higher possum density at this site may have led to greater mistletoe damage cannot be ruled out. However, data from other sites shows that changes in mistletoe condition do not usually directly reflect possum densities, and even a small number of possums may have an effect on mistletoes at some sites (e.g. Hurunui), while significantly greater numbers may have little effect on mistletoes at other sites (e.g. Craigieburn). Thus,

possum density estimates alone do not indicate how susceptible a mistletoe population may be to decline, and a range of factors may influence the consequences of possum damage for plant individuals and populations.

CHAPTER 3: EVIDENCE FOR POSSUM DAMAGE ON NATIVE MISTLETOES

3.1. Mt. Misery: first evidence against possums

3.1.1. 1978-1984

Wilson (1984) first presented data showing that possums contributed to the decline of native mistletoes. Between 1978-1984, Wilson monitored 46 beech mistletoes along an altitudinal transect from the D'Urville Valley (450 m a.s.l.) to above the bushline (1400 m a.s.l.) on Mt. Misery, located at the head of Lake Rotoroa in Nelson Lakes National Park. The dominant vegetation is mixed silver/red beech forest with some mountain beech at higher altitudes (Wilson 1984). The area was colonised by possums about 1965 (Pracy 1974), and prior to 1974, possums were poisoned for skins throughout the study area. In May 1978, DSIR began a capture-recapture study of possums along the mistletoe transect that ended with cyanide poisoning in June 1981.

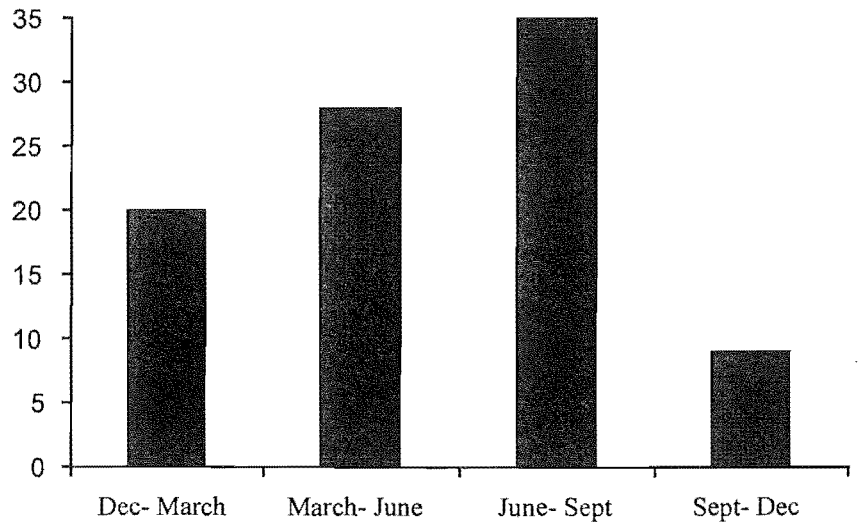
Forty-four mistletoes (18 *Peraxilla colensoi*, 20 *P. tetrapetala*, and 4 *Alepis flavida*) were located in 1977-78, and an additional two *P. colensoi* and two *P. tetrapetala* were found during the study period. Wilson revisited plants every three months and recorded evidence of insect or possum browsing, fruiting and flowering, and plant volumes.

Between 1978- 1982, *P. colensoi* and *P. tetrapetala* were browsed by possums almost once per year on average, and plants were more than 50% defoliated in over half of these attacks (Wilson 1984). Annual variation in possum browse was high, ranging between almost 2 attacks per year in 1978 for *P. tetrapetala* to less than 0.5 attack per year for *P. tetrapetala* in 1979 and for both *Peraxilla* species in 1981. Wilson (1984) suggested that canopy defoliation by caterpillars led to high attack rates in 1978, while plants suffered few attacks following the 1981 possum poisoning. However, the attack rate quickly rose again in 1982, even though possums continued to be live-trapped and killed after the poisoning.

Over the four years, *P. colensoi* plants decreased slightly in mean size, whereas *P. tetrapetala* plant volumes declined more significantly. In contrast, six unbrowsed *P. colensoi* and seven unbrowsed *P. tetrapetala* plants increased in size by an average of 35% and 20% respectively (Wilson 1984).

Wilson continued to monitor the plants quarterly until 1984, and 19 of the 46 plants (41%) had died by 1984 (P.R. Wilson unpublished data). Multiple plants were often attacked during the same time period, but defoliation episodes were not limited to one season (Figure 3.1). Most attacks occurred in winter (June- September), while relatively little browse was recorded in spring (September- December). Field notes also suggested that new shoots were preferentially eaten, and plants in seemingly inaccessible locations were often defoliated.

Figure 3.1. Number of mistletoe plants defoliated by possums during each season between 1978-1984 at Mt. Misery, Nelson Lakes National Park.



3.1.2. 1984-1997

In March 1997, P.R. Wilson and I revisited the Mt. Misery transect to examine the condition of the plants 20 years after initiation of the monitoring project. Of the 27 plants that remained alive in 1984, 14 (52%) had died by 1997 (Table 3.1). Most of the surviving *P. tetrapetala* plants had actually increased in size since 1984, while most of the *P. colensoi* plants were smaller than in 1984.

Table 3.1. Changes in mistletoe condition recorded 1977-1997 at Mt. Misery.

	total plants located	**dead 1977-1984**	**dead 1984-1997**	**larger since 1984**	**smaller since 1984**
A. flavida	4	3	1	--	--
P. colensoi	20	6	9	1	4
P. tetrapetala	22	10	4	7	1

3.1.3. Conclusions from Mt. Misery

Wilson (1984) concluded that "because of browsing by possums which invaded the area less than 20 years ago, *P. tetrapetala* and probably *A. flavida* are in danger of becoming rare and may eventually become extinct on Mt. Misery." Despite relatively low possum densities compared to other forest types (less than 1 possum per hectare; Clout and Gaze 1984), possums still appeared to be severely impacting mistletoes in the area.

Data from 1997 confirm that mistletoes have continued to decline in the Mt. Misery area since the 1980's (in contrast to the rata example discussed in section 1.2.1; these plants declined between 1969-1974 but all remaining plants were still alive in 1990). However, the fact that eight of the 13 living plants (62%) have increased in size may suggest that plants are now improving. Moreover, several plants that appeared dead years ago have re-sprouted and are now healthy individuals, and mistletoes in nearby areas around Lake Rotoiti have also remained healthy during the past few years (D. Butler, personal communication). No possum control has been initiated in the region since 1981, and thus, a decrease in local possum numbers is probably not responsible for this improvement in plant condition.

Additional monitoring would be needed to confirm a long-term upward trend in mistletoe health, since plant conditions can change rapidly year to year. For example, the possum poisoning in 1981 at Mt. Misery only lowered browsing in the short term, and the following year, browsing levels rose again. Wilson (1984) suggested, therefore, that short-term control operations would do little to benefit native plant species such as mistletoes.

3.2. ANECDOTAL EVIDENCE

There are very few eye-witness accounts of possums feeding on mistletoes, although damage on plants has been observed at numerous sites (Ogle 1997). Instead, since Wilson's (1984) quantitative study, anecdotal and circumstantial evidence alone has been used to blame possums for mistletoe decline throughout New Zealand. Ogle and Wilson (1985) first synthesised reports of declining mistletoe distributions coincident with increasing possum densities, and since then, possums have been accepted as the primary source of mistletoe decline (Ogle 1997).

3.2.1. Coinciding possum colonisation and mistletoe decline

Numerous historical reports suggest that native mistletoes were once abundant in regions where they are now rare or locally extinct (Ladley 1994; Ogle 1997). These accounts alone do not prove that possums are the primary source of decline, but Ogle and Wilson (1985) pointed out that mistletoes have suffered the most dramatic declines in areas where possums have been present for a significant period.

For example, possums did not invade the western Waitutu forest and southern Fiordland until the past decade, and four species of mistletoe (*Alepis flavida*, *Peraxilla colensoi*, *P. tetrapetala*, and *Ileostylus micranthus*) are still abundant in the area (Ogle and Wilson 1985). However, browse has been observed on mistletoes in western Waitutu as possums continue to spread across the region (Ogle 1997). Similarly, Moore (1987) suggested that 22 *I. micranthus* were able to survive in an urban Wellington park only because the site was protected from possums by the surrounding residential development. Throughout many parts of the North Island, historical reports suggest that mistletoes were once common but are now rare where possums have been present for a significant time (Ogle and Wilson 1985).

In the Buller and North Westland regions, a correlation exists between *Peraxilla* spp. survival and the recency of possum colonisation (Overmars 1997b), while in South Westland, mistletoes are still common where possum populations have remained sparse and scattered through recent years (Ogle 1997). Many possum-free islands (e.g. D'Urville Island, islands in Lake Waikareiti, Little Barrier Island, and Pigeon Island) also contain numerous mistletoes (Ogle and Wilson 1985; Ogle 1997).

3.2.2. Changes in plant health after protection from browse

The second major line of evidence for possums being the primary cause of mistletoe decline is the improvement of mistletoe plants after they are protected (partially or completely) from possums. At sites throughout New Zealand, the Department of Conservation has banded host trees with aluminium collars or enclosed mistletoes in cages, which usually has led to the recovery of the protected plants (e.g. Courtney 1997; Dopson 1997; Jones 1997a; Barkla and Ogle 1997; Simpson 1997; Walls 1997).

Unfortunately, neither banding nor cages provide long-term solutions to possum damage. Possums can eventually reach banded mistletoes, either over the band on sloping trunks or through the canopy of adjacent host trees. Banding in the Nelson region has not prevented enough browse to enable mistletoes to increase in size (Courtney 1997). Cages may prevent pollinating and dispersing birds from reaching the plants, and cages have to be continually enlarged to accommodate new growth.

Mistletoes have also appeared to benefit from intensive possum control operations (Ogle 1997). For example, a number of *Tupeia antartica* and *Ileostylus micranthus* plants have re-sprouted since possums were eradicated on Kapiti Island in 1983-84 (Atkinson 1992; Sawyer 1997). Possum control in 1994 in the Dingle Valley resulted in no further damage to mistletoes, but no obvious recovery was observed either (Simpson 1997). Milne (1996) found that in Tongariro National Park over a three year period, significantly more *Peraxilla tetrapetala* increased in size in an area with possum control than in a nearby area without control. Various Department of Conservation offices have also collected data to suggest that greater declines in mistletoe condition have occurred in areas without possum control compared to adjacent areas with control operations. Two of these DoC programmes are discussed in detail below.

3.3. Department of Conservation monitoring programs

3.3.1. Eglinton Valley Mistletoe Monitoring

The most systematic and extensive mistletoe monitoring program to date was initiated in 1994 by the Department of Conservation in the Eglinton Valley. This habitat is considered one of the most significant South Island habitats for numerous forest birds, native bats, and threatened plants (Rance and Rance 1995). A possum control operation

was initiated over 6400 hectares of the valley in 1994 to reduce the local possum population by 80% and to maintain control below 20% of the original population.

The main purpose of the mistletoe monitoring program was to determine the success of possum control operations in improving vegetation condition (Rance and Rance 1995). Mistletoes were chosen as the indicator species (rather than monitoring numerous plant species) because the beech forest contained insufficient numbers of a range of palatable species. Also, mistletoes were considered highly palatable, they existed in concentrated populations at a number of known sites in the Eglinton Valley, and observations suggested mistletoes had been declining in the area, presumably because of possum browse (Rance and Rance 1995).

3.3.1.1. Methods

A total of 110 mistletoes (*P. colensoi*, *P. tetrapetala*, and *A. flavida*) were marked on 58 host trees at four sites in the Eglinton Valley: Knobs Flat, Deer Flat, Dore Pass track, and Totara Flat. Both *Peraxilla* species occurred at the first three of these sites, which were located within a possum control area. *Alepis flavida* was monitored only at Totara Flat, which was located outside of the control area. This site was used as the experimental control site, because it was the only known sizeable mistletoe population in the Eglinton Valley outside of the possum control area. This design was problematic because an assumption had to be made that all three species were equally susceptible to possum browsing.

Plants were monitored biannually, during late winter (August-September) and mid-summer (January-February). Size measurements, condition ranking assessment, and photomonitoring were used to assess mistletoe health. The following scale was used to rank mistletoe condition:

1 = 0% defoliated (undamaged)
2 = 1-10% (light damage, some browsing detectable)
3 = 11-25% (moderate damage, browsing easily detectable)
4 = 26-50% (heavy damage)
5 = 50-75% (very heavy damage)
6 = 76-99% (severe damage)
7 = 100% (appears dead, no leaves)
8 = mistletoe disappeared

It was assumed that most visible damage could be attributed to possum browse. Plants were also measured in height, width, and depth to calculate plant volumes. For analysis, plant condition in November 1995 and in September 1996 was compared for each plant, and the plant was classified as having worsened or not (no change or improvement). Plants were categorised according to initial condition, and the numbers of plants that got worse within each category were compared using Chi-square tests.

In addition, 85 of the plants (77%) were visible enough to photograph. Photopoints were established and relocated using aspect and distance measurements from the host trunk. Prints and slides were developed from photos taken with a 55 mm lens and a flash. Mistletoe height from the ground, distance from the trunk, and aspect on the tree were also recorded to assist in relocating plants and to differentiate between multiple plants on a single host.

3.3.1.2. Results

Overall, significantly more *Alepis flavida* plants declined in condition than *Peraxilla* spp. plants (Table 3.2). *A. flavida* plants with low initial damage declined significantly more than *Peraxilla* plants with low damage, but *A. flavida* and *Peraxilla* plants with high initial defoliation had an equally great chance of deteriorating further. For all three species, plants that were more than 50% defoliated at the beginning of the study declined significantly more than plants that began with less than 50% defoliation. This

contrast was the greatest for *P. tetrapetala*. Although no further obvious browse was observed in possum control areas, highly defoliated mistletoes did not appear to recover after possum control was initiated. Instead, damaged plants continued to lose leaves and produce little new growth (C. Rance personal communication).

Table 3.2. Percentage of plants with increasing condition ranking score (i.e. declining health), November 1995- September 1996.

% plants worse	***P. tetrapetala***	***P. colensoi***	***A. flavida***	Chi^2 (species)
Overall	36.3 (n=168)	46.1 (n=102)	70.3 (n=128)	34.34 (p=0.0000)
Started <50% defoliated	20.0 (n=125)	36.5 (n=74)	63.2 (n=76)	38.04 (p=0.0000)
Started >50% defoliated	83.7 (n=43)	71.4 (n=28)	80.8 (n=52)	1.65 (p=0.4385)
Chi^2 (initial condition)	56.2 (p=0.0000)	9.98 (p=0.0016)	4.59 (p=0.0322)	

3.3.1.3. Conclusions

This monitoring program has shown that mistletoe plants outside of a possum control area were significantly more likely to decline in health than plants within a possum control area. However, because the two populations compared were different species, it is possible that the effects of possum control were confounded by interspecific differences between *Alepis flavida* and *Peraxilla* spp. (i.e. in palatability or susceptibility to browse; see section 5.5.3.4). Thus, the overall effect of possum control alone on mistletoe health cannot be deduced from this study.

Plants of all three species inside and outside of the possum control area continued to deteriorate once they were at least 50% defoliated. Thus, protection from browse did not benefit plants that were already unhealthy. These results differ from studies at other sites that have found remarkable recovery of even severely defoliated plants once they were released from possums (e.g. Milne 1996; J.J. Ladley unpublished data from Craigieburn; P.R. Wilson unpublished data from Mt. Misery; C. Rance unpublished data from Mavora Lakes). Some other factor, such as a fungal disease or weather conditions,

may be stressing the already damaged Eglinton mistletoes, preventing them from recovering and thus resulting in their continued decline. Of course, such factors may also have been at least partly responsible for the poor condition of mistletoes at the beginning of the monitoring programme.

3.3.2. Hurunui Mainland Island Monitoring Programme

3.3.2.1. Project background and methods

The South Branch of the Hurunui is located in the southwest corner of Lake Sumner Forest Park in Northern Canterbury. This steep-sided, glaciated valley is approximately 18 km long, and rises from 700 m a.s.l. at its mouth to 940 m a.s.l. near the headwaters. The forest is composed primarily of mountain beech, with extensive areas of mixed red and silver beech forest on the terraces (Grant *et al.* 1996).

In 1995, Hurunui was designated a Mainland Island by the Department of Conservation, and an integrated management and research program was developed for a 10 km stretch in the mid section of the valley encompassing 4200 hectares. The proposed project included wild animal control as well as monitoring various native species.

As part of the monitoring component, in 1996, 55 mistletoe "sites" (mistletoes on a single host tree; 11 *Alepis flavida* and 44 *Peraxilla tetrapetala*) containing 275 individuals were permanently marked. Twenty-six sites (six *A. flavida* and 20 *P. tetrapetala*) were located within a possum control area (less then 0.3 possums per hectare after 2 years of poisoning), while the remaining 29 sites were located outside this treatment area (Grant *et al.* 1998). In March 1997 and at six month intervals thereafter, each site was scored on the same eight point scale used in the Eglinton study (see section 3.3.1).

3.3.2.2. Results and conclusions

Significantly more mistletoe "sites" improved or remained in the same condition within the possum control area than outside of the control area between March 1997 and March 1998 (Table 3.3), even though pre-control possum densities were low (trap-catch rate=3.7%; see section 2.3.2). All but one site was less than 50% defoliated at the

beginning of the study, and thus, initial condition was unlikely to have been a confounding factor, as it was for mistletoes in the Eglinton Valley (see above). Of the 15 plants that improved in condition in both areas, only 3 individuals improved by more than one category (one *A. flavida* and one *P. tetrapetala* in the control area and one *A. flavida* in the untreated area). In contrast, nine of the 18 plants that declined in condition (two *P. tetrapetala* in the control area and one *A. flavida* and six *P. tetrapetala* in the untreated area) deteriorated by more than one category.

Table 3.3. Changes in plant condition ranking scores at Hurunui, March 1997- March 1998.

	Area with possum control (n=26)	**Area without control (n=29)**
% plants worse	11.50	51.72
% plants same	50.00	34.48
% plants better	38.46	13.79
Chi^2 = 10.06, p=0.0015		

These results suggest that mistletoe health does improve when possums are controlled. However, possum densities were not high even before control, and plants have only been monitored for one year. Thus, more data are needed to establish a long-term trend in mistletoe condition. This study also indicates that mistletoes may decline rapidly but may require a much longer time period to recover.

3.4. EVIDENCE AGAINST POSSUMS AS THE PRIMARY AGENT OF DECLINE

Mistletoes have a non-random distribution that is probably related to a number of biotic and abiotic factors including herbivory, the distribution and abundance of pollinating and dispersing birds (Ladley and Kelly 1996; Ladley *et al.* 1997), the availability of host species, disturbance patterns, and the availability of light, water and nutrients (Norton and Reid 1997). There are exceptions to the general trend in anecdotal evidence of decreases in mistletoe health and abundance with possum colonisation, which suggests that other factors in addition to herbivory influence mistletoe distribution.

Many possum-free islands with suitable mistletoe hosts lack mistletoes for unknown reasons (Ogle and Wilson 1985), and the now extinct *Trilepidea adamsii* once survived on several islands, where possums could not have contributed to their decline (Norton 1991). In the Nelson area, possums have been noted to damage mistletoes, but no correlation exists between the duration of possum occupation and the persistence of mistletoes (Courtney 1997).

Similarly, over the past six years, little browse has been observed at Craigieburn, despite the presence of possums since the 1960's. Populations of *Alepis flavida* and *Peraxilla tetrapetala* have been intensively studied since 1992, but browse has not been observed on most plants (Ladley 1994), and the mortality rate among the studied plants (excluding experimentally damaged plants) has been just 1.8% per year (D. Kelly unpublished data).

Mistletoes have been widely presumed to be highly palatable mostly because of foreign examples: stock in the Northern Hemisphere regularly browse mistletoe, and in their native habitat, Australian possums prefer mistletoes to their host trees (Barlow and Wiens 1977; Freeland and Winter 1975; Reid 1997). However, no gut analyses in New Zealand have shown that possums consume substantial quantities of mistletoe foliage. Mason (1958) found no mistletoe in possum stomachs from the Orongorongo Valley, but mistletoes were probably rare (or even absent) in the area. The only known finding of a New Zealand mistletoe in possum guts was by Owen and Norton (1995), who showed that *Peraxilla colensoi* constituted only 0.5% of annual food intake of possums in the Upper Haast Valley. *P. colensoi* was not highly preferred relative to its abundance in the forest. Owen and Norton (1995) thus concluded that possums were not selectively removing mistletoes in this area, either because more attractive food sources were available or because the study was conducted during an unusually low flowering and fruiting year.

Owen (1993) also found that possums consumed only 2% of leaf area on 20 monitored *P. colensoi* plants in the Upper Haast Valley. Insects browsed more than possums (4% of leaf area), and leaf abscission caused the loss of 46% of leaf area (Owen 1993). Despite the presence of possums in the area for at least 30 years, mistletoes are still locally abundant, and thus, possums do not yet appear to have limited mistletoes in this region. However, the small proportion of plants that were browsed by possums lost

significantly more leaves than unbrowsed plants, which indicates that possum herbivory does have significant implications for damaged plants (Owen 1993).

3.5. CONCLUSIONS

Wilson (1984) first suggested that possum browse was the primary cause of mistletoe decline. Beech mistletoes on Mt. Misery in Nelson Lakes National Park declined drastically between 1978 and 1984, and they have continued to decline over the ensuing 13 years. Similar declines have been observed throughout New Zealand, and possums have been blamed in most cases. The most abundant evidence for the impacts of possums is anecdotal reports of declining mistletoe populations coincident with the spread of possum populations, which suggests that mistletoes may eventually disappear from most of New Zealand apart from areas unsuitable for possum colonisation. However, the pattern does not always fit, as some regions contain both abundant mistletoes and possums. Owen (1993) quantitatively showed that possums actually remove little leaf area from mistletoes in certain regions such as the Upper Haast Valley.

The major problem with the evidence to date is that although possum damage on plants has been observed at numerous sites, no data exist to conclusively prove causation rather than correlation alone. Other changes, such as extensive forest clearance and a decline in native bird populations, may have been simultaneously encouraging the decline of mistletoe populations. Browse obviously does have a negative impact on plant health, as numerous studies have shown that caged and banded plants can increase in size and reproductive output, and Owen (1993) showed that browsed plants are less healthy than unbrowsed mistletoes. However, when we shift our focus to the population level, results are less conclusive. Mortality rates have been high at Mt. Misery, and plants have improved in possum control areas. In contrast, mortality and browse are low at Craigieburn and Haast despite the presence of possums. Thus, the overall importance of possums to mistletoe populations relative to other factors has been difficult to determine. The remainder of this thesis presents detailed data on the impact of possums at four South Island sites (Craigieburn, Lake Ohau, Eglinton Valley, and Waipori Gorge).

CHAPTER 4: PATTERNS OF MISTLETOE LEAF LOSS AND IMPLICATIONS FOR PLANT HEALTH

4.1. INTRODUCTION

One of the primary goals of this research project was to quantify the amount of leaf biomass that mistletoe plants lose annually and to identify the causes of this loss. A total of 60 mistletoe plants in six different populations were monitored over a year to measure patterns of leaf loss in two different geographical areas for each of the three mistletoe species (*Alepis flavida*, *Peraxilla colensoi*, and *Peraxilla tetrapetala*) . In particular, this chapter will investigate the following questions:

1. How much damage do insects and possums inflict on mistletoes? What is their relative importance to total leaf loss, and does this vary according to season, site location, or species? How important is leaf abscission and what factors may cause leaves to be lost?

2. How is leaf damage distributed across an individual plant? How is it distributed across a population of plants? Do patterns of damage differ for insects and possums, and if so, what are the consequences for plants? In other words, could the spatial and temporal distribution of browse be as important as the total leaf area lost?

3. Does new growth compensate for leaves lost during the year? What is the average flux in leaf area that plants experience annually, and how does this vary across sites and species? Do plants that are browsed by possums have significantly different leaf losses and growth from unbrowsed plants?

4.2. METHODS

4.2.1. Identifying types of leaf damage

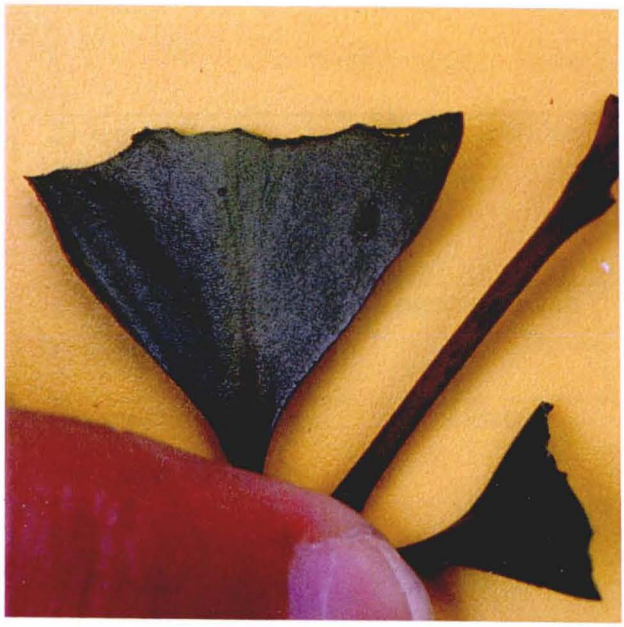
Meads (1976) described how possum browse could be distinguished from insect damage on northern rata (*Metrosideros robusta*). Possums left torn and jagged leaf stubs, while insects often left holes and wavy, clean-edged patterns (caterpillars) or straight, finely milled edges (stick insects). Owen (1993) described similar patterns on *Peraxilla colensoi*: possums left torn edges and often ate leaves to their bases, while insects left semi-circular cuts and clean edges. The semi-circular bites of stick insects may be most frequently confused with possum browse (de Lange 1997).

Plate 4.1 shows typical patterns of possum and insect damage on mistletoes. As well as torn leaf edges (Plate 4.1.a), possums tended to leave rows of petioles (Plate 4.1.b), bite marks on branches, and sometimes torn twigs. Browse on flowers and fruits was also occasionally observed (Plate 4.1.c), primarily on *Alepis flavida* at Craigieburn. Possum browse also usually affected entire branches or areas of a plant, rather than only a few scattered leaves, which made possum damage easier to distinguish from insect damage. Patterns of damage were similar on all species.

Insect damage patterns were similar to Meads' (1976) description of rata leaf damage (Plate 4.1.d). No detailed work has been conducted on invertebrates associated with endemic mistletoes, but Patrick and Dugdale (1997) identified a number of specialist and generalist moths that feed on *Peraxilla* species (Table 4.1). Caterpillars tended to create wavy edges and holes in leaves, and *Zelleria* spp. often created a white, silk cocoon between overlapping leaves, leaving a heart-shaped indentation. Caterpillars of *Declana griseata*, *Tatosoma agrionata*, and *Zelleria* spp. were observed on leaves at various sites. Damage from stick insects was characterised by clean cut edges.

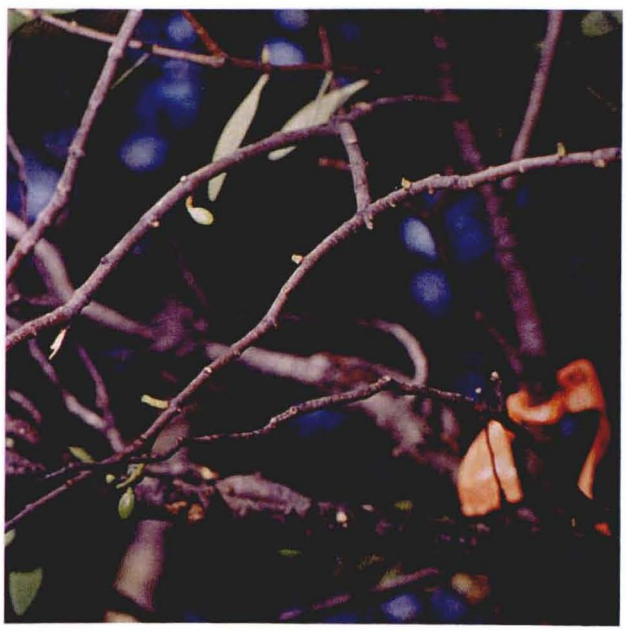
Plate 4.1.a. Possum damage on a *P. colensoi* leaf at Waipori in December 1996, characterised by the torn edge. **b.** Row of petioles left after a possum attack on a *P. tetrapetala* plant at Craigieburn in February 1998. **c.** Possum browse on fruits of an *A. flavida* plant at Craigieburn in March 1998. **d.** Insect damage on a *P. colensoi* plant at Waipori in December 1996.

a)



b)

c)



d)

Table 4.1. Moth species that damage *Peraxilla* spp. according to Patrick and Dugdale (1997).

Species	Family	Characteristics
Declana griseata	Geometridae	specialist moth on leaves; large, purplish-black larvae; adults emerge August-Nov. & March-May; up to 988 m a.s.l.
Tatosoma agrionata	Geometridae	specialist moth on leaves; green larvae; adults emerge July-May; up to 900 m a.s.l.
Zelleria sphenota	Yponomeutidae	leaf-miner; green larvae (9 mm); create silken cocoons between leaves; adults emerge August-Feb.; up to 900 m a.s.l.
Zelleria maculata	Yponomeutidae	same as above but also attacks flower buds and fruits
Catamacta gavisana *Apoctena flavescens* *Ctenopseustis obliquana* *Planotortrix excessana*	Tortricidae	generalist, polyphagus leafrollers; do not depend on mistletoes for survival

Although most damage could be confidently identified as either insect or possum browse, some leaves were difficult to categorise, particularly at the beginning of the study when some damage was fairly old. If damage could not be confidently attributed to one or the other, insect damage was always used as the default option. Thus, possum damage may have been slightly underestimated. However, Meads (1976) estimated that less than 3% of the browsing reported as possum damage in his study on northern rata could have been caused by insects, suggesting that the error in identification is probably low. Furthermore, the frequent revisits for this study would probably have reduced this uncertainty, as recent possum damage is easier to recognise than older browse.

Damage from fungi and other diseases was not recorded in this study. *Peraxilla colensoi* plants at Eglinton and Waipori and plants in both *Alepis flavida* populations

developed black spots on their leaves. A fungus may have been responsible for these marks (A.L.J. Cole personal communication), but the pathogen has not been identified, and its effects on leaf abscission and plant health are unknown.

4.2.2. Experimental design

In February 1997, ten plants were selected haphazardly from six populations: *Alepis flavida* at Craigieburn and Eglinton, *Peraxilla colensoi* from Eglinton and Waipori Gorge, and *Peraxilla tetrapetala* from Craigieburn and Lake Ohau. Study plants had to be accessible using a 6-foot ladder and large enough to possess sufficient branches suitable to tag and map. On each plant, ten branches approximately 15- 25 cm long were tagged with coloured wire and the leaves on each branch were drawn. A total of 17,336 leaves were originally recorded in February 1997 with an additional 8349 leaves added during the year (Table 4.2). Damage on each leaf was recorded on a 6-point scale: 0 = no damage, 1 = 1- 25% gone, 2 = 26- 50% gone, 3 = 51- 75% gone, 4 = 76- 99% gone, and 5= 100% gone. Damage was attributed to possums or insects, or to abscission if the leaf completely disappeared.

Table 4.2. Number of leaves recorded on leaf maps from February 1997 to February 1998.

Species/site	**No. leaves recorded 2/97**	**No. new leaves added 2/97-2/98**	**Total leaves recorded**
A. flavida, Craigieburn	3736	1452	5188
A. flavida, Eglinton	2172	769	2941
P. colensoi, Eglinton	2660	863	3523
P. colensoi, Waipori	2145	1290	3435
P. tetrapetala, Craigieburn	3306	2067	5373
P. tetrapetala, Ohau	3317	1908	5225
TOTAL	17,336	8349	25,685

Plants were revisited every three months (May, August, November 1997, and February 1998) and new leaf damage was recorded. At the same time, the plants were

photographed and measured, and visual estimates of percent defoliation and crown density were recorded (see Chapter 6 for further details on these methods).

In addition, parts of five other *Alepis flavida* and five *Peraxilla tetrapetala* plants at Craigieburn were enclosed in wire cages (20 mm holes) lined with mesh netting (18 mm holes) from April 1997 to April 1998. These cages were designed to exclude possums without greatly altering light levels or access by insects. The number of leaves on a large, tagged branch within each cage were counted every two months to get an estimate of annual leaf flux in the absence of possum browse.

4.2.3. Data analysis

4.2.3.1. Mean leaf loss

The damage on each leaf from abscission, insects, and possums over each three-month period was calculated using the midpoint of the damage category (0 = 0% gone, 1 = 12.5% gone, 2 = 38% gone, 3 = 63% gone, 4 = 87.5% gone, or 5 = 100% gone). The difference between the leaf's damage at the previous monitoring time and the current time was considered the total damage for that leaf over the three month period. Mean leaf loss from abscission, insects, and possums on each branch was then calculated by summing the total area lost on recorded leaves over each three-month period and dividing by the total area of leaves present during that period. Mean leaf loss on each plant was estimated by summing all damage and number of leaves on the ten marked branches, rather than by averaging mean branch losses, because branches on a plant had quite different leaf numbers, particularly as new growth emerged. Mean leaf losses for plants in a population, however, were calculated by averaging the ten mean plant losses.

The number of leaves counted present during a three month period included leaves that appeared during that interval, since the leaves could already have had insect or possum damage before they were first recorded at the end of the period. However, new leaves that abscised before they were recorded obviously could not be included, and thus, damage from abscission may be slightly underestimated. This methodology also assumes that new leaves were present and at risk for most of the time period during which they appeared, so very small (and thus obviously brand new leaves) were not

recorded as present until the following season. Annual losses could not be calculated by adding the three-month averages because new leaves appeared and accumulated damage during the study. Instead, annual rates of leaf loss were calculated by multiplying the four seasonal rates of loss, so that annual loss (L_A) = 1 - [(1-L_1)*(1-L_2)*(1-L_3)*(1-L_4)], where L_x= leaf loss at revisit number x and L_0= start. The percentage of leaves lost on branches and plants that died or disappeared during the year was also estimated for each population. The total leaf loss on plants was then calculated by adding the percentage of leaves lost on missing plants and branches plus the percentage mean leaf loss multiplied by the proportion of plants and branches that remained through the year.

4.2.3.2. Variation in leaf loss

Coefficients of variation (c.v.'s) were used to estimate variation in insect and possum damage between branches on each plant and between plants in a population. Within plant c.v.'s for insect loss and possum loss were calculated by dividing the standard deviation of mean branch losses by the mean branch loss for each plant. Between plant c.v.'s were calculated for each population by dividing the standard deviation of mean insect and possum losses on each plant by the mean plant loss. Whereas mean plant losses were calculated by summing the total damage and number of leaves on all ten branches, c.v.'s were calculated using the average of the 10 mean branch losses to compare variations between branches.

The coefficients of variation for insect and possum damage were then compared using two-sample t-tests assuming equal variances to estimate within and between plant variation. Paired t-tests could not be used because some plants and some populations did not suffer possum browse during every season, which resulted in an undefined c.v. Coefficients of variation for seasonal loss from insects and possums were also calculated by dividing the standard deviation of the four seasonal mean losses by the mean loss per season for each population. These c.v.'s for each population were compared using a paired t-test. *P. tetrapetala* at Ohau was omitted from all three analyses of variation because no possum browse was observed on these plants during the study.

4.2.3.3. Annual flux in leaf area

Annual changes in leaf area were calculated for each plant by subtracting total leaf loss from the number of new leaves that grew between February 1997 and February 1998. This change in leaf area was then expressed as a percentage of the initial number of leaves on each plant in February 1997. Analyses of variance on S-Plus (version 3.1, Statistical Sciences, Inc., Seattle, WA, USA) were used to test differences in leaf area change between: 1) species, 2) sites, and 3) plants with and without possum damage.

The total amount of damage and the number of new leaves were also compared separately among species and between plants with and without possum damage. The mean annual damage for each plant was divided by the initial number of leaves on the plant in February 1997 to give a relative measure of damage. (However, because new leaves that appeared during the study could also accumulate damage, these figures do not represent an absolute annual damage figure. These figures should instead be considered relative measures that can be compared against each other). An analysis of variance test on S-Plus was then used to test for a difference in mean damage between species or between plants with and without any recorded possum damage during the year. Similar methods were used to calculate the differences in mean new leaf growth among species and between browsed and unbrowsed plants.

Annual leaf fluxes for the 10 caged plants at Craigieburn were also compared to fluxes for uncaged plants at the same site. For caged plants, the annual flux was calculated by subtracting the number of leaves on the plant at the end of the year from the initial number of leaves and then dividing by the initial number of leaves. The fluxes for the five caged plants of each species were then averaged. New growth and damage could not be compared separately because leaves were only counted, not mapped, and thus, it was often difficult to determine the exact number of new leaves.

4.3. RESULTS

4.3.1. Plant and branch loss

Two study plants died between February 1997 and February 1998. One *Alepis flavida* plant at Eglinton was completely defoliated by possums between February and May and then died and fell from its host by August. A *Peraxilla colensoi* plant at Waipori Gorge

disappeared from its host between November 1997 and February 1998, and no evidence indicated the cause of its death.

In addition, 41 of the 600 mapped branches disappeared during the study: 17 branches on four *Alepis flavida* plants at Eglinton, 23 branches on eight *Peraxilla tetrapetala* plants at Lake Ohau, and one branch on a *Peraxilla colensoi* at Waipori Gorge. Wind or snow may have been responsible for many of the missing branches at Lake Ohau, because extensive wind damage was observed at this site between May and August when 21 of the 23 branches broke off. In contrast, 16 of the 17 branches on *A. flavida* at Eglinton were eliminated between August and November. The four plants had suffered severe defoliation from possums, and branches had few or no leaves left when they broke off.

An additional four study branches died during 1997 on two *P. tetrapetala* plants at Lake Ohau. Both plants appeared to be suffering from lack of water and many leaves on the plant were brown and wilted. Branches and plants that disappeared or died during the study were excluded from analysis of leaf loss for time periods after their disappearance. Table 4.3. shows the total percentage of recorded leaves at each site that were lost through plant and branch loss.

Table 4.3. Approximate percentage of total mapped leaves lost on plants and branches that died or disappeared at each site from Feb. 1997- Feb. 1998.

Species/site	**Plants lost**	**Branches lost on plants that survived**	**Total % leaf loss from branch and plant loss**
A. flavida, Craigieburn	0/10	0/100	0
A. flavida, Eglinton	1/10	17/90	27
P. colensoi, Eglinton	0/10	0/100	0
P. colensoi, Waipori	1/10	1/90	11
P. tetrapetala, Craigieburn	0/10	0/100	0
P. tetrapetala, Ohau	0/10	27/100	27

4.3.2. Mean leaf loss

Table 4.4 shows average plant leaf loss from abscission, insects, and possums during the four monitored periods for each population. In every population, abscission accounted for by far the most leaf loss, while insect and possum damage both accounted for relatively low losses. All 60 study plants had abscised leaves during at least one season, while 51 plants (87.9% of the 58 plants that survived the entire year) had some abscission during all four seasons. Mean abscission rates for plants varied between 0-100% of plant leaf area over any three month period. Although abscission losses varied widely, the mean three-month loss was 11.0%. *Alepis flavida* at Eglinton had the highest average leaf abscission between February and May (52.4% per plant), while *Peraxilla tetrapetala* at Craigieburn experienced the lowest mean abscission (1.9% per plant) during the same time period.

All plants were also damaged by insects, but only 25 of the 58 plants that survived the year (43.1%) had insect damage during all seasons. Sixteen plants were not damaged by insects during one season, and an additional 17 plants were not damaged in two or three seasons. Insect damage accounted for the mean loss of between 0- 8.9% of leaf area on individual plants over a three-month period, and the average three-month loss for a plant was 0.70%. *Peraxilla colensoi* at Eglinton had the highest mean insect damage during each season (Table 4.4), and all 10 plants were damaged during all four seasons.

Possum browse contributed little to overall leaf loss (Table 4.4). Only 19 of the study plants (32%) had any possum damage during the entire year, and just seven of these plants were browsed during more than one season. No possum browse was observed on *P. tetrapetala* at Lake Ohau, although possum damage was observed on *A. flavida* at the site (but these plants were not monitored in detail for this study). Possum damage over three months varied between 0- 26.89% of leaf area on a plant, and among browsed plants, the average three-month loss from possums was 0.46% of plant leaf area.

Table 4.4. Mean leaf losses per plant (% of total recorded leaf area) in each population from abscission, insect damage, and possum damage during three-month monitoring periods from Feb. 1997 to Feb. 1998. The highest losses from each cause are in bold.

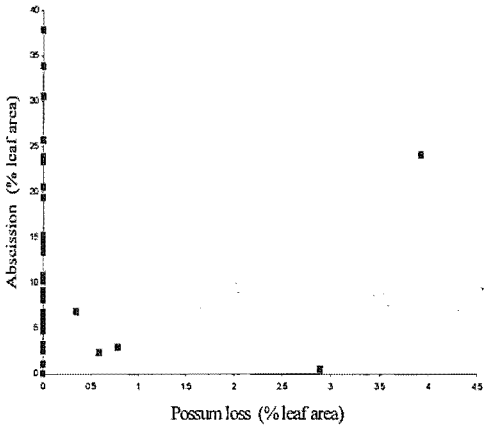
species/site	Feb.- May			May- Aug.			Aug.- Nov.			Nov.- Feb.		
	Abs.	**Insect**	**Possum**	**Abs.**	**Insect**	**Possum**	**Abs.**	**Insect**	**Possum**	**Abs.**	**Insect**	**Possum**
A. flavida, Craigieburn	4.44	0.07	0.29	4.26	0.04	0.14	16.65	0.06	0.39	19.24	0.74	0.03
A. flavida, Eglinton	**52.42**	0.32	**6.78**	47.56	0.09	0	31.27	0.54	0.29	8.59	1.24	0
P. colensoi, Eglinton	11.24	3.41	0.54	5.40	1.06	0	4.45	0.75	0.09	12.95	**3.61**	0.09
P. colensoi, Waipori	3.85	0.51	0.54	8.88	0.33	0.33	2.48	0.45	0	5.72	1.69	0.42
P. tetrapetala, Craigieburn	1.93	0.02	0.03	2.08	0.03	0	2.61	0.04	0	3.42	0.51	0.99
P. tetrapetala, Lake Ohau	2.28	0.52	0	2.22	0.16	0	2.05	0.26	0	8.39	0.46	0

Three *A. flavida* plants at Eglinton lost between 10-20% of their mapped leaves to possums and suffered heavy defoliation (i.e. abscission). The remaining seven *A. flavida* plants at this site were also severely defoliated by possums, but little possum browse was recorded on leaf maps because most leaves were completely removed and recorded as abscised. One of these plants was 100% defoliated between February and May, but all leaves had abscised and thus no possum browse was actually present on the plant. Bite marks, torn branches, and leaves browsed to petioles lying under the plant all suggested that possums were responsible for the defoliation.

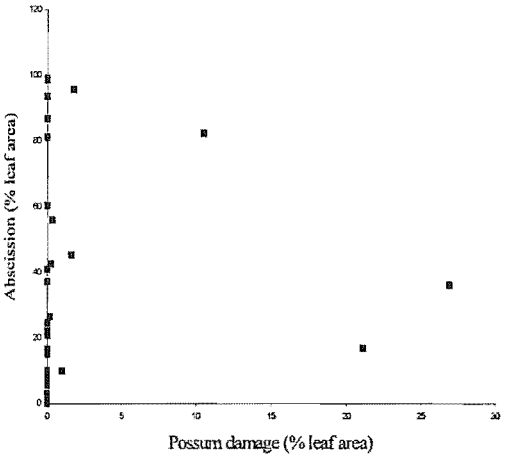
Although much abscission appeared to be cryptic possum damage (i.e. secondary possum damage resulting from the abscission of browsed leaves), scatter plots of abscission versus possum damage for each population show that in most cases, total abscission rates do not increase linearly with recorded possum damage on leaf maps (Figure 4.1). A linear relationship existed only for *P. colensoi* at Waipori (Figure 4.1.d; $F=4.84$, $p=0.0346$). Although data for these tests were not normally distributed and thus failed to meet the assumptions for a linear regression, the point of this test was to determine if visible possum damage could be used to predict cryptic abscission rates and no such clear trends were found.

Figure 4.1. Scatter plots of leaf abscission (% leaf area lost per plant per season) versus possum damage (% leaf area lost per plant per season). Linear regressions showed a significant relationship at only one site, (d) *P. colensoi* at Waipori (y = 1.4316x + 4.5676 , R^2=0.1247, n=36).

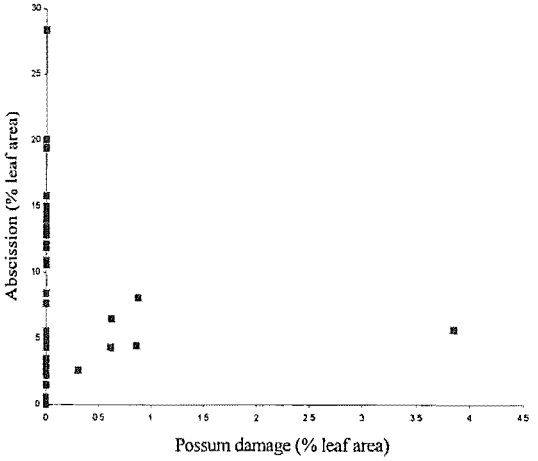
a) *A. flavida*, Craigieburn



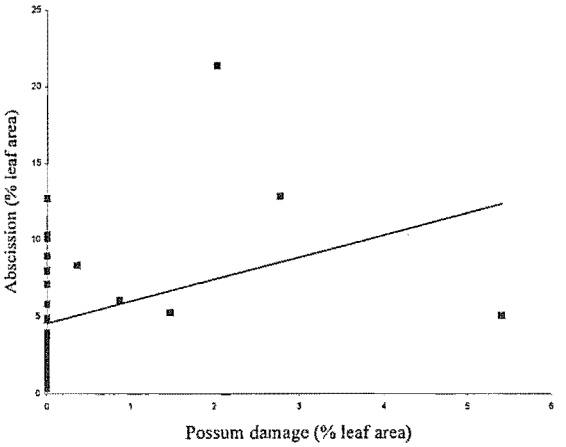
b) *A. flavida*, Eglinton



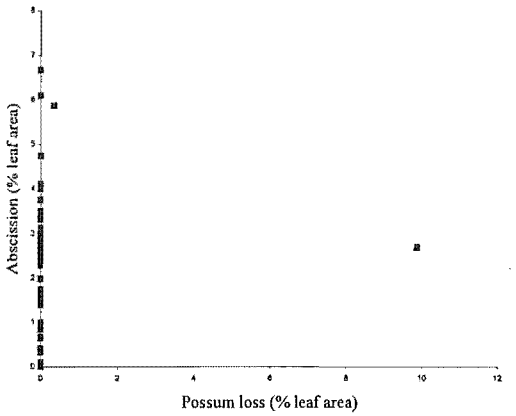
c) *P. colensoi*, Eglinton



d) *P. colensoi*, Waipori



e) *P. tetrapetala*, Craigieburn



Over the entire year (Feb. 1997- Feb. 1998), leaf abscission accounted for much more of total leaf loss than insects or possums for all six of the mistletoe populations in this study (Table 4.5). *Alepis flavida* at Eglinton had significantly more loss from abscission and possum damage than the other populations, and *Peraxilla colensoi* at Eglinton had the highest insect damage. Mean annual estimates of leaf loss across all six populations were calculated as approximately 32.7% of leaf area lost to abscission, 2.8% lost to insects, and 1.8% consumed by possums. Owen (1993) calculated remarkably similar rates on 40 *Peraxilla colensoi* plants in the Upper Haast Valley over nine months: plants lost an average of 45.7% of leaf area to abscission, 4.1% to insects, and 2.1% to possums. The death and loss of branches and plants contributed to leaf loss in three populations, and this loss was most significant for *P. tetrapetala* at Lake Ohau and *A. flavida* at Eglinton.

Table 4.5. Mean annual leaf loss from abscission, insects, possums, and plant and branch loss for each study population from Feb. 1997 to Feb. 1998.

Species/site	Mean annual leaf loss (%) from			Total mean leaf loss (%)	Total plant/ branch loss (%)	Total estimated leaf loss (%)*
	Abscis.	Insects	Possums			
A. flavida, Craigieburn	38.39	0.91	0.85	40.15	0	40.15
A. flavida, Eglinton	84.32	2.18	7.05	93.55	27	95.29
P. colensoi, Eglinton	30.16	8.57	0.72	39.45	0	39.45
P. colensoi, Waipori	19.45	2.95	1.28	23.68	11	32.08
P. tetrapetala, Craigieburn	9.67	0.60	1.02	11.29	0	11.29
P. tetrapetala, Ohau	14.26	1.39	0	15.65	27	38.42
overall mean	32.71	2.77	1.82	37.30	11.50	44.51
P. colensoi, Haast**	45.73	4.05	2.12	51.90	0	51.90

*Total loss equals % loss from branches/plants plus the % mean leaf loss multiplied by fraction of branches that remained through the year.
**From Owen (1993).

4.3.3. Variation in leaf loss

Insects damaged most plants during most seasons; only 58 cases (plants per season) out of 236 total cases had no insect browse. Insects never severely damaged plants, and the highest insect browse recorded during three months was only 8.9% mean leaf loss on a *P. colensoi* plant at Eglinton between February and May. In contrast, only 28 cases (representing only 19 plants) of the 236 cases had any possum browse, and possums frequently caused severe damage to plants. Three *Alepis flavida* plants at Eglinton suffered between 10- 30% mean leaf loss from possums over three months. An additional plant in this population suffered 100% defoliation between February and May, almost certainly from possums (see above).

The coefficients of variation (c.v.'s) for mean insect loss were significantly lower than c.v.'s for mean possum loss for both branches within plants and for plants within populations (Table 4.6). The within plant c.v. for mean possum loss was greater than the within plant c.v. for insect loss in 14 of the 19 cases when both insect browse and possum browse occurred on a plant during that season. Insect browse was evenly

spread across leaves on most branches of each plant, while possums tended to browse in concentrated areas of plants (i.e. only on certain branches). Moreover, the difference in variation between insect and possum damage was especially large between plants, and the mean c.v. for possum loss was over twice the mean c.v. for insect loss between plants. In all 16 cases where at least some possum browse occurred on the sample plants, the c.v. for possum loss was greater than the c.v. for insect loss.

Coefficients of variation for insect and possum damage between seasons were both low and not significantly different (Table 4.6). However, only seven of the nineteen plants browsed by possums were browsed during more than one season, indicating that possums attack plants sporadically rather than continually over the year. Almost all plants were browsed by insects in multiple seasons.

Table 4.6. A comparison of coefficients of variation for possum and insect damage on branches within each plant, on sampled plants within each population, and between seasons for each population. *P. tetrapetala* at Ohau was omitted because no possum browse was observed.

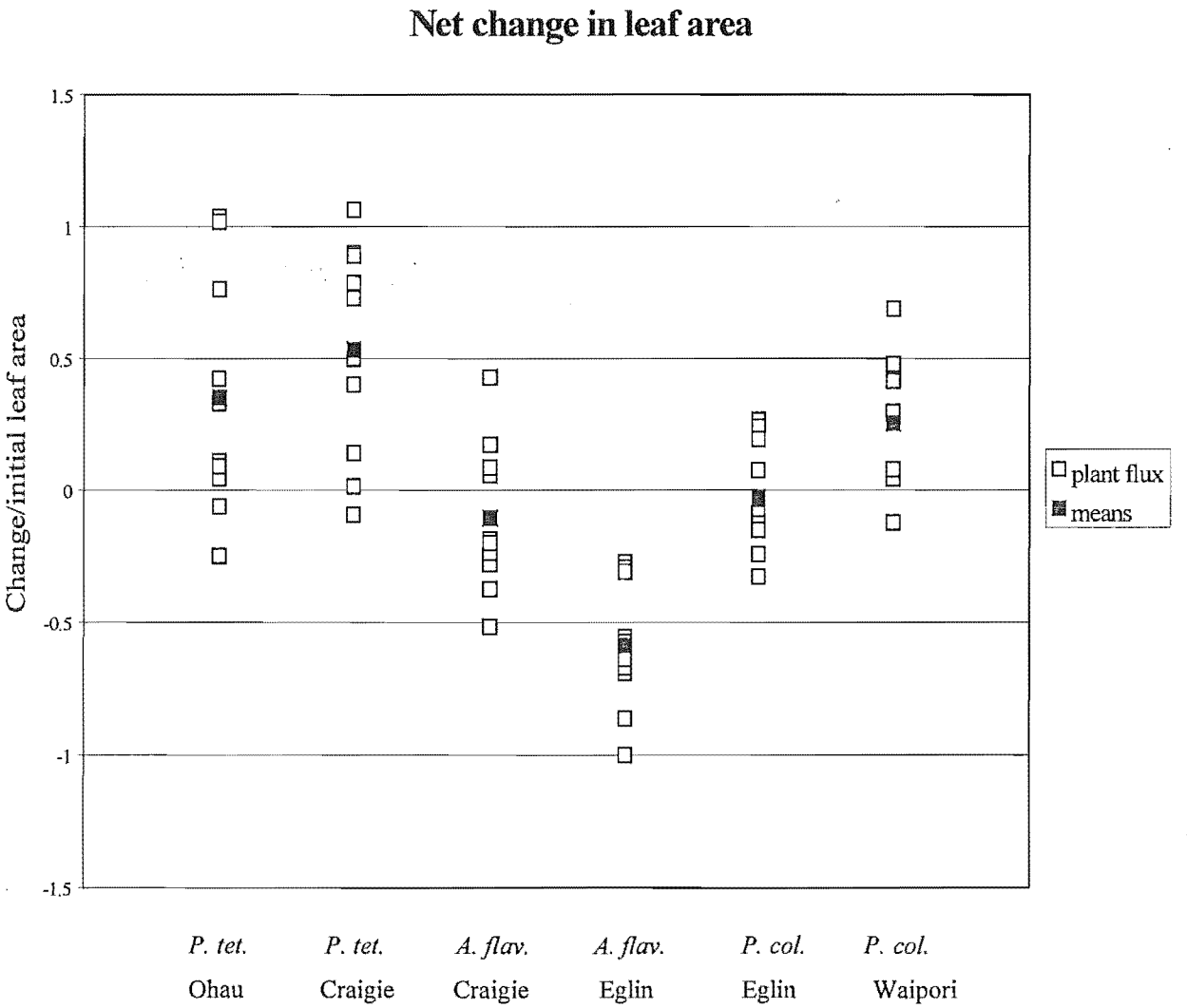
	Mean c.v.		**Sample size**		**T-statistic**	**P-value**
	Insect	**Possum**	**Insect**	**Possum**		
within plants	1.94	2.63	142	28	-4.38	0.0000
between plants	1.17	2.74	20	16	-8.27	0.0000
between seasons	1.03	1.08	5	5	-0.11	0.9146

4.3.4. Annual flux in leaf area

Both *Peraxilla tetrapetala* populations had positive mean net changes in leaf area during the year (Figure 4.2). Only one plant at Craigieburn and two plants at Ohau had negative net changes, and three *P. tetrapetala* plants had a net growth of more than 100% of their initial leaf areas. The *Peraxilla colensoi* population at Waipori also had a positive mean change in leaf area, but *Peraxilla colensoi* at Eglinton had a small negative mean net change. Only one plant at Waipori had a negative change, while six *P. colensoi* at Eglinton had negative changes in leaf area. Both *Alepis flavida* populations lost significantly more leaves than they grew during the year (Figure 4.2).

Six of the Craigieburn plants suffered negative changes, and all of the ten Eglinton *A. flavida* plants had negative net changes, ranging between -27.3% and -100%.

Figure 4.2. Leaf flux (change in leaf area divided by the initial leaf area on mapped branches) for each plant is plotted by population. Mean leaf flux for each population is designated by a black square.



Mean net change in leaf area was significantly different among the three species (Table 4.7) and between the four sites (Ohau mean= 0.35, Craigieburn= 0.21, Eglinton= -0.31, Waipori= 0.25; F=9.73, p=0.0000). The three species had both significantly different relative damage levels and significantly different relative amounts of new growth. *A.*

flavida had both the lowest relative mean new growth and the highest relative mean damage, while *P. tetrapetala* had both the highest relative new growth and the lowest relative damage.

Table 4.7. Differences among the three mistletoe species in mean damage, mean new growth, and annual net change. All means are expressed as percentages of initial leaf number in February 1997.

Species	Number of plants	Mean % damage	Mean % new leaves	Mean % net change
A. flavida	20	70.42	35.84	-34.58
P. colensoi	20	43.18	54.46	11.28
P. tetrapetala	20	19.08	63.21	44.13
F-value		35.87	4.34	15.86
p-value		0.0000	0.0176	0.0000

Plants at all sites that suffered possum damage during the year on average had a negative net change in leaf area, whereas the unbrowsed plants had a positive mean change over the year (Table 4.8). Browsed plants had significantly more damage than unbrowsed plants during the year, but browsed and unbrowsed plants did not have significantly different levels of new growth. An analysis of variance showed that the interactions between both species and possum damage ($F=0.17$, $p=0.8447$) and site and possum damage ($F=0.61$, $p=0.5487$) were not significant (see also Table A1, Appendix 1).

Table 4.8. Differences in relative mean damage, mean new growth, and net change between plants browsed by possums and those not browsed by possums. All figures are expressed as percentages of initial number of leaves in February 1997.

	Number of plants	**Mean % damage**	**Mean % new leaves**	**Mean % net change**
Browsed plants	19	61.66	45.65	-16.01
Unbrowsed plants	41	36.15	53.73	17.58
F-value		12.59	0.85	13.60
p-value		0.0008	0.3618	0.0006

The five caged *A. flavida* plants at Craigieburn had a mean annual leaf flux of -23.8%. One of the *P. tetrapetala* plants died during the study, but the remaining four plants had a mean flux of +36.0%. Both of these means were similar to fluxes for uncaged plants of the same species (Table 4.7). The fluxes for caged plants may be overestimates of damage, because leaves that abscised were always counted as -1, regardless of any previous browse on leaves (c.f. uncaged plants on which abscised leaves were considered a loss of the amount of undamaged leaf area). However, any damage (i.e. insect browse) on leaves other than complete loss was not recorded on caged plants, and thus, the caged and uncaged plant fluxes may be relatively comparable.

4.4. Discussion

4.4.1. Mean leaf loss

4.4.1.1. Insect loss

The results from this study correspond extremely well with Owen's (1993) estimates of leaf loss for *P. colensoi* at Haast: all of the mistletoe populations in this study lost significantly more leaf area to abscission than to either insect or possum damage (Table 4.5). Insect damage was relatively low at all sites over each season (Table 4.4). Lepidoptera and stick insects have generally not been recorded significantly damaging mistletoes, but cases of severe browse have occasionally been reported, particularly on

already stressed plants (de Lange 1997). Further studies are needed to determine whether insect damage poises a serious threat to certain populations (de Lange 1997).

Peraxilla colensoi at Eglinton had the highest insect damage during every season, and damage peaked during summer (November- May). Patrick and Dugdale (1997) have suggested that an abundance of mistletoes in the Eglinton Valley may have enabled dense populations of specialist moths to survive there, but mistletoe densities are not nearly as high in Eglinton as at other sites, such as Ohau and Craigieburn, where insect damage is relatively low. Conversely, if mistletoe numbers in the area have been recently reduced, host-specific moths may have intensified feeding on the remaining plants (de Lange 1997). Ironically, Meads (1976) also suggested that possum control could contribute to higher insect damage, because possums are known to feed on invertebrates, especially during winter (Owen and Norton 1995). Environmental variables might also regulate insect numbers. For example, most of the specialist moths associated with mistletoes have only been recorded at altitudes below 900- 1000 metres (see Table 4.1). In addition, at Craigieburn and Lake Ohau, an undescribed parasitoid has been observed infecting *Zelleria* spp., which is one of the most common insects that damages mistletoe flowers and leaves. This parasitoid may thus account for the low rates of insect attack on mistletoe leaves at these two sites.

4.4.1.2. Possum damage and associated abscission

The leaf map results suggest that at the population level, possums do not consume significant amounts of mistletoe foliage, as the maximum annual leaf loss to possums among the six populations was only 7.1% on *A. flavida* at Eglinton. However, all of the monitored *A. flavida* plants at Eglinton were severely defoliated between February and August. These plants also lost an average of 84.3% of leaf area to abscission during the year (Table 4.5), which indicates that much abscission was cryptic (i.e. secondary) possum damage. Possums may increase abscission rates by: 1) damaging leaves which are then more likely to abscise (see section 5.2); 2) eating (or removing) entire leaves; 3) destroying or dislodging leaves as they move on the plant; and 4) causing physiological stress (Payton 1983). The abscission of browsed leaves thus may make it difficult to estimate total possum damage, particularly using this method of monitoring.

Numerous studies have found a correlation between the occurrence and intensity of possum browse and defoliation (Meads 1976; Leutert 1988; Owen 1993; Cowan *et al.* 1997b). Although at the population level, high abscission was correlated with high possum damage on *A. flavida* at Eglinton in this study, at the individual plant level, abscission did not increase predictably with possum damage (Figure 4.1). Populations containing plants that were only lightly browsed (*A. flavida* and *P. tetrapetala* at Craigieburn and *P. colensoi* at Eglinton) probably were not affected enough by browse to have much secondary damage via abscission. Moreover, the small number of browsed plants in these populations made the relationship between abscission and possum damage difficult to discern. In the population with heavy possum damage (*A. flavida* at Eglinton) the highest rates of abscission were often associated with low possum damage, simply because these plants were almost completely defoliated and thus had very few leaves left to show possum damage. Thus, abscission only seems to increase linearly with possum damage when possum browse is intermediate (both in terms of the number of plants browsed and in the intensity of defoliation). The only population in this study where abscission increased predictably with possum damage was *P. colensoi* at Waipori, which did experience a medium level of possum browse (Figure 4.1.d).

4.4.1.3. Other causes of abscission

High abscission rates should not automatically be attributed to possums, since high levels of leaf abscission could also result from wind and snow break, heavy insect damage, diseases, drought, or other factors influencing plant health (de Lange 1997). In other words, leaf abscission does not necessarily represent average "natural" leaf loss, but may partly reflect significant stresses to plant health. In this study, wind and snow break damaged mistletoes at Lake Ohau, while insect damage or a fungal pathogen may have been important in the Eglinton Valley (see section 4.4.3). At least three species of pathogenic fungi have been recorded in association with dead or dying mistletoes, but it is unclear whether fungal outbreaks represent a serious threat to plants (de Lange 1997). The strong winds between May and August at Lake Ohau did not appear to increase leaf abscission rates on retained branches, but many branches and entire sections were lost from plants, which greatly increased overall leaf loss (Table 4.5).

Deciphering the causes of leaf abscission may be straightforward in some cases but less clear when multiple factors have confounding effects. For example, heavily browsed trees may develop more open canopies and thus be more susceptible to insect damage, diseases or climatic extremes (Green 1984; Payton 1988; Cowan *et al.* 1997b). Furthermore, the difficulty of assessing confounding factors such as wind, insects, drought and diseases may have contributed to disagreement over the severity of possum damage. Meads (1976) observed 20% mortality of northern rata trees between 1969-1974, which he ascribed to possum browse, and he predicted continued mortality as damage was concentrated on the remaining trees (see section 1.2.1). However, Cowan *et al.* (1997b) returned to these trees in the 1990's and found that no more had died in the subsequent 20 years, despite periods of above average possum densities in the area. They suggested that a severe drought combined with possum damage during Meads' study may together have resulted in the high observed mortality.

4.4.2. The importance of heterogeneity

Although average leaf losses from insects and possums both accounted for relatively small proportions of total leaf loss, the distribution of this damage across branches within each plant and between plants within a population could also influence plant health. Insect damage was very even and low across most plants, but possum browse only affected a small proportion of the plants and often inflicted severe defoliation. Possum browse was also more patchy within plants, and only certain branches or sections were usually browsed. In addition, possums usually did not damage plants during more than three months of the year. Thus, although possum browse on the population level was spread over the year, browse on individual plants was extremely variable through time. Thus, insect browse was probably a predictable stress for most plants, while possum damage was much less predictable, more concentrated, and thus, potentially more detrimental to plant health.

Other studies have shown that possums only feed on select individuals but tend to browse these plants heavily, while insect damage is much lighter and more homogenous. For example, Cowan *et al.* (1997b) monitored fourteen rata (*Metrosideros robusta*) trees in the Orongorongo Valley, and found that only half of the trees were heavily browsed by possums over a four year period. The trees were scored using a five point browse category scale (0 = no browse to 4 = dead), and the seven

heavily browsed trees had significantly higher browse scores than the seven lightly browsed or unbrowsed trees. Insects damaged all trees but caused only minor leaf loss (Cowan *et al.* 1997b).

Similarly, Wilson (1984) reported that both *Peraxilla* species averaged almost one possum attack per year at Mt. Misery between 1978- 1982. In over half of these attacks, more than 50% of the plant was defoliated. *Alepis flavida* suffered an average of almost 0.5 attacks per year, and about 75% of these plants were more than 50% defoliated (Wilson 1984). Owen (1993) also showed that only 7 of 40 *P. colensoi* plants suffered from any possum browse in a 9-month study in South Westland. The plants with possum damage had significantly greater total leaf losses than the unbrowsed plants, although only one plant received heavy damage (26.4% of leaf area; Owen 1993). In contrast, insects damaged all plants but only caused the loss of between 0.5- 14.3% of leaf area.

Crawley (1989) suggested that vertebrate herbivores are important to plants simply because they can consume more total biomass than invertebrate herbivores. In addition, the relative importance of vertebrate and invertebrate herbivory to plants may shift across time and space as environmental conditions and the distribution and abundance of organisms change (see Palmisano and Fox 1997). However, insect attacks on mature plants are rarely fatal (although they may cause plant mortality at earlier developmental stages; Weis and Berenbaum 1989). In this study, possums did not actually consume more mistletoe biomass on average than insects at the population scale, but the herbivores did have very different feeding patterns within a population. Thus, the amount of damage on individual plants is probably more important to plant growth and survival than the population mean rate of leaf loss.

Owen (1993) also noted that the patchiness of possum browse could "increase the potential damage that any given number of possums may cause." Unpredictable and often severe possum attacks, even if infrequent, may cause some plants to die. For species such as mistletoes that have slow reproductive rates and long life spans, these deaths could over time lead to a slow decline at the population level. Thus, even in areas where possums do not appear to be having obvious effects on mistletoes, the populations may be affected over longer time spans.

The heterogeneity of possum browse has important implications for how we monitor mistletoes, and perhaps other species that are browsed by possums. Because only a small subset of plants may be damaged, a large number of plants should be monitored to guarantee that the mistletoes chosen do not over or under-estimate the amount of damage occurring over the population. Second, plants should be monitored frequently enough to ensure that sporadic browsing events are represented, particularly since browse patterns may be difficult to detect after new growth emerges. Monitoring techniques will be discussed in more detail in Chapter 6.

4.4.3. Annual flux in leaf area: implications for plant health

Lindroth (1989) suggested that the impact of herbivory on plants is influenced by four factors: 1) characteristics of the plant (e.g. growth rates, nutrient status, life span, etc.); 2) environmental variables (e.g. resource availability); 3) consumption patterns (e.g. severity, type, and timing of damage); and 4) interactions between these three factors. All of these factors appear to influence overall patterns of mistletoe leaf loss and the consequences of possum herbivory for mistletoes.

First, the three mistletoe species differed in their overall leaf fluxes, which could either be influenced by differing levels of possum damage on the three species, or by variable responses to browse by the three species. *Alepis flavida* sustained the most possum damage and had negative mean annual changes in leaf area at both sites. This species is more palatable to possums than *Peraxilla* spp. (see section 5.5.3.4), and the large losses on Eglinton plants were probably a result of the heavy possum browsing at that site. However, possums cannot definitively be blamed for the negative leaf changes observed at Craigieburn, especially since caged plants also experienced mean net losses in leaf area. *A. flavida* also have a shorter life span than *Peraxilla* plants (Powell and Norton 1994), and thus, more *Alepis* plants may be senescing than *Peraxilla* plants at any one time. However, if recruitment is sufficient, populations should not decrease as new plants quickly mature and replace older ones. Alternatively, some other factor, such as a fungal disease or a drought associated with the El Niño weather pattern, may have affected plant health.

Environmental variables also appeared to affect leaf loss, as changes in leaf area significantly differed among the four study sites. Both populations at Eglinton had negative changes, but while *A. flavida* suffered from heavy possum damage, *P. colensoi* plants were located within a possum control area and were almost entirely unbrowsed. This population had the highest level of insect damage in the study (Table 4.5), and a fungal pathogen might also be contributing to leaf loss. Johnston *et al.* (1994) found an undescribed species of *Diaporthe* fungus on leaves from both *Peraxilla* spp. at this site, and although the impact of this fungus is unknown, species of *Diaporthe* cause blights, cankers, and diebacks in other woody plants. In contrast, de Lange (1997) describes *Diaporthe* as a saprophyte, and suggests that *Fusarium* spp. is the most likely fungus to cause the death of *P. colensoi*. More research is needed to identify potential pathogens, but regardless, plants may be particularly vulnerable to fungal damage if their defences are already reduced by stresses, such as possum damage or drought (de Lange 1997; Johnston *et al.* 1994).

Thirdly, plants with possum damage had a significantly more negative mean net change in leaf area than unbrowsed plants, which suggests that features of possum herbivory (i.e. patchy, severe attacks) lead to more detrimental effects on plant health than insect browse, since all plants were browsed by insects. Owen (1993) also found that *P. colensoi* plants that suffered possum damage had significantly greater total leaf losses; the majority of unbrowsed plants had a positive net change in leaf area over his nine-month study, while most browsed plants had a negative net change.

However, in both this study and Owen's (1993) study, browsed and unbrowsed plants significantly differed in the amounts of total damage they received but not in amounts of new growth. If browse does not influence the growth of new leaves, plants may be able to recover quickly from browsing episodes once the browsing pressure is removed. Defoliation of woody species usually decreases plant growth rather than inducing compensatory growth (Lindroth 1989; Danell *et al.* 1994), but normal spring flushes may gradually replace lost leaves. However, this replacement only occurs annually, and thus, repeated defoliation may increase the likelihood of plant mortality (Pekelharing *et al.* 1998a). Meads (1976) found that moderately browsed northern rata trees grew enough new leaves to sufficiently cover previous browse, but heavily browsed trees continued to accumulate damage on new leaves. Data from the Eglinton Valley also indicate that severely damaged mistletoes tend to continue to decline even after

browsing pressure is removed (see section 3.3.1). In addition, the timing of browse could greatly influence the effects of herbivory on plant health (Lindroth 1989; Danell *et al.* 1994), since damage directly after budbreak may be more detrimental to plants than browse during other seasons (Payton 1985; see section 5.4.3.1).

Cowan *et al.* (1997b) suggested that rata trees may survive heavy possum browsing only if possum densities fluctuate and remain at low levels for sufficient intervals. They suggest that periods of low browsing may have enabled the rata plants that Meads studied to recover (see section 1.2.1), since possum densities in the Orongorongo Valley remained below average for periods of more than two to three years (Cowan *et al.* 1997b). Payton (1985) showed similar recovery for southern rata (*Metrosideros umbellata*) when possums were controlled. Milne (1996) also suggested that mistletoes on banded trees (i.e. protected from possums) might require at least five years to recover. Short-term declines in possum populations are therefore unlikely to benefit mistletoes (Meads 1976; Cowan *et al.* 1997; Simpson 1997). Wilson (1984) suggested that mistletoes at Mt. Misery sustained little damage after a poisoning operation in 1981 killed most possums in the area, but by the following year, damage had again increased. In the Hurunui River Valley, possum control has benefited mistletoes after just one year, but again, the plants appear to be recovering slowly (Grant *et al.* 1998; see section 3.3.2).

J. Ladley and D. Norton are currently investigating the effects of defoliation on mistletoe health by defoliating *P. tetrapetala* and *A. flavida* plants at Craigieburn. Defoliation did not appear to affect plants during the first year, and all of the plants--including those completely defoliated--remained alive one year later (J.J. Ladley and D.A. Norton unpublished data). However, it is not clear how repeated defoliation will affect plant health, since repeated stripping of new growth might prevent mistletoe plants from recovering. Pekelharing *et al.* (1998a) found that repeated defoliation greatly increased mortality rates for five other palatable plants in beech forests. Furthermore, Ladley and Norton defoliated plants in October, prior to the mistletoe growth season, which may enable plants to produce new leaves from buds during the following months. Such damage may be less likely to affect plant health than damage over the spring and summer (see section 5.4.3.1).

4.5. Conclusions

The results presented in this chapter suggest the following conclusions:

1. Mistletoe plants vary greatly in the amount of leaf area they lose annually, but abscission almost always accounts for the greatest loss. However, numerous factors may increase abscission rates, including possum browse, heavy insect damage, wind and snow break, and diseases. Thus, although possums and insects accounted for low levels of recorded damage in this study, these data may be underestimates because of abscised leaves.

2. Possum damage is extremely patchy within individual plants, between plants in a population, and over time, while insect browse is much more even across individuals and populations and through time. Possums severely defoliated some plants (although these losses were sometimes recorded as abscission since leaves were often completely removed), while insects rarely caused serious leaf loss. Thus, although possums on average accounted for less leaf loss than insects, the spatial and temporal heterogeneity of possum browse may affect individual plants more than homogeneous insect browse.

3. Plants that were browsed by possums on average lost more leaves than they could produce during the year, while unbrowsed plants experienced net growth. However, possums did not appear to affect the growth of new leaves, and thus browsed plants may be able to recover once possums are removed for a sufficient recovery period.

This chapter has suggested that possums may affect mistletoes primarily because of their patchy browsing patterns, but the sources of this heterogeneity remain unclear. In the next chapter, I will discuss why possums browse certain individuals and not others by examining in more detail the factors that influence leaf loss at various scales.

CHAPTER 5: FACTORS INFLUENCING HERBIVORY AND LEAF ABSCISSION

5.1. INTRODUCTION

In Chapter 4, I discussed the variation in leaf loss between mistletoes within a population and between plants from different species and locations. In this chapter, I now turn to the sources of this variation; that is, why do certain plants lose more leaves than others, and in particular, why do possums prefer some plants over other ones?

I examine some of the primary factors that could influence leaf loss at five hierarchical levels: between leaves, branches, plants, sites, and species. First, factors that directly influence the probability of damage on an individual leaf are discussed. Obviously, plants with many leaves prone to damage will have high rates of leaf loss. At the next level, I examine whether leaf loss is related to branch position, and thirdly, what factors influence variation in leaf loss among individuals of a population. Finally, differences between conspecific individuals from different regions and between co-occurring individuals of the three beech mistletoe species are discussed.

5.2. VARIATION BETWEEN LEAVES

5.2.1. Methods for leaf level analyses

At the leaf level, I examined how leaf age, previous leaf damage, and insect galls affected leaf loss. Leaf damage was recorded on mapped leaves and calculated at three month intervals between February 1997 and February 1998 on 60 plants in six populations, as described in Chapter 4 (see section 4.2.2). At the beginning of the study (February 1997), insect galls were also recorded on *Peraxilla tetrapetala* leaves, and leaves on all species were classified as either "new" (growth new in summer 1996-97) or "old" (previous growth).

Leaves that appeared during a given time period were included in analyses of possum and insect damage, because leaves could accumulate damage even before they were first recorded. However, new leaves were not included in tests of abscission, because leaves that emerged and abscised within a single monitoring period could not be recorded. Abscised leaves, as well as leaves on branches and plants that died or disappeared during the study, were excluded from analysis at subsequent times for all leaf-level analyses.

Data at the leaf level could not be normalised because of the large number of zeros (i.e. cases where no damage occurred on a leaf; especially common for possum browse). Therefore, the effect of leaf age on leaf loss was analysed using the non-parametric Kruskall-Wallace one-way analysis of variance test on Statistix (version 1.0, Analytical Software, St. Paul, MN, USA). Tests were conducted for each of the study populations at three of the four time periods (February-May 1997, August-November 1997, and November 1997-February 1998). Analyses were not conducted for the May-August 1997 season because not enough new leaves appeared during this season to examine them as a separate age category, and examinations of the other three seasons were sufficient to study trends in leaf loss based on the continued ageing of leaves over the year. Loss due to abscission, insect browse, and possum browse were each analysed separately, and leaves were grouped into six age categories: already old in February 1997; new growth in February 1997; or first appeared in May, August, November 1997, or February 1998. When an age category contained less than 10 leaves, those leaves were added to the next youngest age category.

To determine if damaged leaves were more likely to abscise than undamaged leaves, leaves were classified into five categories according to their missing leaf area at each monitoring date: 1) undamaged, 2) 1- 25% gone, 3) 26- 50% gone, 4) 51- 75% gone, and 5) 76- 99% gone. Chi-square tests were used to compare the number of leaves that abscised in each damage category for each population over each time period. When a Chi-square cell contained fewer than five cases, the damage categories were combined.

Chi-square tests were also conducted to determine if leaves with galls abscised more frequently then leaves without galls. Only leaves present in February 1997 were included in this analysis. When a Chi-square cell had fewer than five cases, categories of gall numbers were combined.

5.2.2. Results

5.2.2.1. Effect of leaf age on probability of abscission

Arithmetic means for leaf losses of each age category (Tables 5.1.a, b, and c) should not be compared across seasons or sites, as previous damage and total number of leaves varied. However, the means do indicate relative differences in damage between leaves of different ages on the same plants.

Between February and May, significantly more old leaves (growth prior to summer 1996-97) abscised than new leaves (new in summer 1996-97) in all but one population (Table 5.1.a). *Alepis flavida* plants in the Eglinton Valley had significantly higher losses from abscission on new leaves than on old leaves, but the average abscission rate for all leaves was higher than for other populations (see Table 4.4).

Table 5.1.a. Differences in leaf abscission between new and old leaves, February- May 1997, and results from Kruskall-Wallace analysis of variance tests.

Species/site	Leaf age	No. leaves	Mean abscission (% leaf area)	F-statistic	Pr(F)
A. flavida, Craigieburn	old 2/97	1619	9.33	97.84	0.0000
	new 2/97	2118	0.44		
A. flavida, Eglinton	old 2/97	739	43.06	6.54	0.0106*
	new 2/97	1411	43.24		
P. colensoi, Eglinton	old 2/97	738	15.93	84.81	0.0000
	new 2/97	922	4.62		
P. colensoi, Waipori	old 2/97	697	7.60	65.12	0.0000
	new 2/97	1448	1.51		
P. tetrapetala, Craigieburn	old 2/97	1279	2.68	5.97	0.0146
	new 2/97	2037	1.20		
P. tetrapetala, Lake Ohau	old 2/97	834	5.29	48.09	0.0000
	new 2/97	2460	1.32		

*Significantly more abscission on new leaves than on old.

Between August and November, old leaves were again significantly more likely to abscise than new leaves in four of the six populations (Table 5.1.b). Thus, even as new

leaves aged, they still appeared less likely to abscise than the oldest leaves. The Eglinton *A. flavida* population again had extremely high levels of abscission among all leaves, and the probability of abscission did not differ significantly between new and old leaves. Only the Lake Ohau *P. tetrapetala* population had enough leaves appear between May and August to analyse them as a separate group (both species at Craigieburn had less than 15 leaves appear during this time, which were grouped with leaves new in February 1997). This newest group of leaves abscised most frequently in this population, but the oldest leaves still had higher abscission rates than leaves new in February 1997.

Table 5.1.b. Differences in leaf abscission between new and old leaves, August-November 1997, and results of Kruskall-Wallace analysis of variance tests.

Species/site	Leaf age	No. leaves	Mean abscission (% leaf area)	F-statistic	Pr(F)
A. flavida, Craigieburn	old 2/97 new 2/97 & 5/97	1327 2079	30.27 5.33	156.41	0.0000
A. flavida, Eglinton	old 2/97 new 2/97	115 183	73.74 78.52	3.15	0.0769
P. colensoi, Eglinton	old 2/97 new 2/97	528 849	10.52 1.60	69.88	0.0000
P. colensoi, Waipori	old 2/97 new 2/97	490 1344	8.92 1.96	57.60	0.0000
P. tetrapetala, Craigieburn	old 2/97 new 2/97, 5/97 & 8/97	1194 1993	5.56 0.60	77.37	0.0000
P. tetrapetala, Lake Ohau	old 2/97 new 2/97 5/97 & 8/97	553 1877 127	7.05 1.84 12.00	34.35	0.0000

This trend continued between November and February, with the oldest leaves still more likely to abscise than summer 1996-97 growth in every population (except *A. flavida* at Eglinton where the two categories had to be combined because so few leaves remained; Table 5.1.c). However, in every population except *A. flavida* at Eglinton, leaves that appeared between August and November were also more likely to abscise than leaves that emerged during the past summer. In the *A. flavida* and *P. tetrapetala* populations at Craigieburn, these newest leaves also abscised more often than the oldest leaves, but these sample sizes were small (Table 5.1.c).

Table 5.1.c. Differences in leaf abscission between new and old leaves, November 1997- February 1998, and results from Kruskall-Wallace analysis of variance tests.

Species/site	Leaf age category	No. leaves	Mean abscission (% leaf area)	F-statistic	Pr(F)
A. flavida, Craigieburn	old 2/97	900	48.21	218.89	0.0000
	new 2/97 & 5/97	1958	15.12		
	11/97	11	81.82		
A. flavida, Eglinton	old & new 2/97	34	29.02	7.14	0.0078
	11/97	498	13.58		
P. colensoi, Eglinton	old 2/97	459	23.36	83.65	0.0000
	new 2/97	831	3.01		
	11/97	663	18.27		
P. colensoi, Waipori	old 2/97	395	11.57	42.58	0.0000
	new 2/97	1223	1.69		
	11/97	1147	8.88		
P. tetrapetala, Craigieburn	old 2/97	1120	10.44	57.98	0.0000
	new 2/97	1963	2.11		
	5/97, 8/97 & 11/97	22	22.73		
P. tetrapetala, Lake Ohau	old 2/97	503	24.74	45.17	0.0000
	new 2/97	1781	7.82		
	5/97 & 8/97	109	8.71		
	11/97	983	9.22		

5.2.2.2. Effect of leaf age on insect damage

Between February and May, insect damage varied significantly with leaf age in only two populations: *Peraxilla colensoi* at Eglinton had twice as much insect damage on new leaves as on old leaves, while *Peraxilla tetrapetala* at Ohau had four times as much damage on the newest leaves as on older leaves (Table 5.2.a). The other four populations had non-significant differences in insect damage based on leaf age.

Table 5.2.a. Differences in insect damage on new and old leaves, February- May 1997, and results from Kruskall-Wallace analysis of variance tests.

Species/site	Leaf age	No. leaves	Mean damage (% of leaf area)	F-statistic	Pr(F)
A. flavida, Craigieburn	old 2/97	1619	0.04	0.85	0.4286
	new 2/97 & 5/97	2120	0.08		
A. flavida, Eglinton	old 2/97	739	0.14	3.42	0.0645
	new 2/97	1411	0.40		
P. colensoi, Eglinton	old 2/97	738	1.80	27.61	0.0000
	new 2/97	922	3.76		
P. colensoi, Waipori	old 2/97	697	0.52	1.43	0.2314
	new 2/97	1448	0.41		
P. tetrapetala, Craigieburn	old 2/97	1279	0	2.51	0.1129
	new 2/97 & 5/97	2037	0.07		
P. tetrapetala, Lake Ohau	old 2/97	834	0.49	14.10	0.0000
	new 2/97	2460	0.40		
	5/97	148	1.87		

Three populations had significantly different levels of insect damage on old and new leaves between August and November (Table 5.2.b). *Alepis flavida* at Eglinton had browse only on leaves that appeared since August. *P. tetrapetala* at Ohau also had the most insect damage on its newest leaves and little damage on its oldest leaves. *P. colensoi* at Eglinton had more insect browse on leaves new in February than on those new in November, but the oldest leaves again sustained the least damage.

Table 5.2.b. Differences in insect damage on new and old leaves, August- November 1997, and results of Kruskall-Wallace analysis of variance tests.

Species/site	Leaf age	No. leaves	Mean damage (% of leaf area)	F-statistic	Pr(F)
A. flavida, Craigieburn	old 2/97	1327	0.06	0.02	0.9914
	new 2/97 & 5/97	2079	0.06		
	11/97	11	0		
A. flavida, Eglinton	old 2/97	115	0	7.31	0.0008
	new 2/97	183	0		
	11/97	511	1.09		
P. colensoi, Eglinton	old 2/97	528	0.22	13.31	0.0000
	new 2/97	849	1.07		
	11/97	663	0.46		
P. colensoi, Waipori	old 2/97	490	0.23	1.78	0.1666
	new 2/97	1344	0.36		
	11/97	1180	0.58		
P. tetrapetala, Craigieburn	old 2/97	1194	0	2.47	0.0829
	new 2/97	1993	0.05		
	5/97, 8/97 & 11/97	22	0		
P. tetrapetala, Lake Ohau	old 2/97	553	0.09	6.68	0.0002
	new 2/97	1877	0.22		
	5/97 & 8/97	127	0		
	11/97	983	0.65		

During the final time period, November 1997-February 1998, every population had significantly more insect damage on new leaves (new in November 1997 or February 1998) than on old leaves (present in February 1997; Table 5.2.c), except *A. flavida* at Eglinton, which had very few remaining old leaves. Three populations had more damage on leaves new in November than on leaves new in February 1998, while one population had more on the newest leaves than on November leaves. Four of the populations had more damage on leaves from summer 1996-97 than on their oldest leaves, but these differences were never great.

Table 5.2.c. Difference in insect damage on new and old leaves, November 1997-February 1998, and results of Kruskall-Wallace analysis of variance tests.

Species/site	Leaf age	No. leaves	Mean damage (% of leaf area)	F-statistic	Pr(F)
A. flavida, Craigieburn	old 2/97	900	0.06	90.44	0.0000
	new 2/97 & 5/97	1958	0.03		
	11/97 & 2/98	1450	1.92		
A. flavida, Eglinton	old & new 2/97	24	0	2.11	0.1197
	11/97	498	1.13		
	2/98	258	0.83		
P. colensoi, Eglinton	old 2/97	459	0.30	183.17	0.0000
	new 2/97	831	0.53		
	11/97	663	5.94		
	2/98	200	12.49		
P. colensoi, Waipori	old 2/97	395	0.80	51.84	0.0000
	new 2/97	1223	0.85		
	11/97	1147	3.28		
	2/98	110	1.82		
P. tetrapetala, Craigieburn	old 2/97	1120	0.05	81.95	0.0000
	new 2/97, 5/97 & 8/97	1978	0.10		
	11/97 & 2/98	2052	1.16		
P. tetrapetala, Lake Ohau	old 2/97	503	0.08	24.72	0.0000
	new 2/97	1781	0.20		
	5/97 & 8/97	109	0		
	11/97	983	1.77		
	2/98	769	0.46		

5.2.2.3. Effect of leaf age on possum browse

The sampled plants from the *Peraxilla tetrapetala* population at Lake Ohau experienced no possum damage during the entire study period and were excluded from this analysis. Between February and May, the Craigieburn *P. tetrapetala* plants also suffered no possum damage, while the remaining four populations all had significantly more possum browse on new leaves than on old leaves (Table 5.3.a).

Table 5.3.a. Differences in possum damage on new and old leaves, February- May 1997, and results of Kruskall-Wallace analysis of variance tests.

Species/site	Leaf age	No. leaves	Mean damage (% leaf area)	F-statistic	Pr(F)
A. flavida, Craigieburn	old 2/97	1619	0	4.23	0.0145
	new 2/97 & 5/97	2120	0.42		
A. flavida, Eglinton	old 2/97	739	1.59	54.98	0.0000
	new 2/97	1411	8.57		
P. colensoi, Eglinton	old 2/97	738	0	7.27	0.0071
	new 2/97	922	0.69		
P. colensoi, Waipori	old 2/97	697	0.07	9.87	0.0017
	new 2/97	1448	0.86		
P. tetrapetala, Craigieburn	old 2/97	1279	0	--	--
	new 2/97 & 5/97	2037	0		

Between August and November, no possum browse was observed again on the Craigieburn *P. tetrapetala* population and on *P. colensoi* at Waipori Gorge (Table 5.3.b). *P. colensoi* at Eglinton had only 2 old leaves damaged by possums. Including the 11 leaves that appeared between August and November on *A. flavida* at Craigieburn, no significant difference could be detected between browse on different aged leaves. However, by excluding these leaves, significantly more possum damage was detected on new leaves than on old ones (F=6.63, p=0.0101). *A. flavida* at Eglinton only had possum browse on leaves new in summer 1996-97.

Table 5.3.b. Differences in possum damage on new and old leaves, August- November 1997, and results of Kruskall-Wallace analysis of variance tests.

Species/site	Leaf age	No. leaves	Mean damage (% leaf area)	F-statistic	Pr(F)
A. flavida, Craigieburn	old 2/97	1327	0.05	2.24	0.0805
	new 2/97 & 5/97	2079	0.52		
	11/97	11	0		
A. flavida, Eglinton	old 2/97	115	0	3.45	0.0316
	new 2/97	183	0.82		
	11/97	511	0		
P. colensoi, Eglinton	old 2/97	528	0.14	0.74	0.4838
	new 2/97	849	0		
	11/97	663	0.13		
P. colensoi, Waipori	old 2/97	490	0	--	--
	new 2/97	1344	0		
	11/97	1180	0		
P. tetrapetala, Craigieburn	old 2/97	1194	0	--	--
	new 2/97 5/97,	1993	0		
	8/97 & 11/97	22	0		

Between November and February, no possum damage occurred on *A. flavida* at Eglinton, probably because possum control operations were completed in the area during November. Browse was only observed on the newest growth in the remaining four populations, and the damage was significant in three cases (Table 5.3.c). *A. flavida* at Craigieburn only had 1 recorded leaf that was browsed by a possum during this time.

Table 5.3.c. Differences in possum damage on new and old leaves, November 1997-February 1998, and results of Kruskall-Wallace analysis of variance tests.

Species/site	Leaf age	No. leaves	Mean damage (% leaf area)	F-statistic	Pr(F)
A. flavida, Craigieburn	old 2/97	900	0	0.66	0.5777
	new 2/97 & 5/97	1958	0		
	11/97 & 2/98	1450	0.06		
A. flavida, Eglinton	old & new 2/97	24	0	--	--
	11/97	498	0		
	2/98	258	0		
P. colensoi, Eglinton	old 2/97	459	0	6.56	0.0003
	new 2/97	831	0		
	11/97	663	0		
	2/98	200	0.63		
P. colensoi, Waipori	old 2/97	395	0	8.14	0.0000
	new 2/97	1223	0		
	11/97	1147	0.96		
	2/98	110	0		
P. tetrapetala, Craigieburn	old 2/97	1120	0	29.99	0.0000
	new 2/97, 5/97 & 8/97	1978	0		
	11/97 & 2/98	2052	1.57		

5.2.2.4. Summary of effects of leaf age on leaf area loss

Table 5.4 summarises the results of the Kruskall-Wallace tests between leaf age and leaf area loss to abscission, insects, and possums. In most cases, old leaves were significantly more likely to abscise than young leaves, while insect and possum damage were both more common on new leaves.

Table 5.4. Summary of significant relationships between leaf age and leaf area loss from abscission, insects, and possums on each population during three seasons from Feb. 1997 to Feb. 1998. A slash signifies no relationship, "O" equals more loss on old leaves, "N" equals more loss on new leaves, and n/a signifies no data.

Species/site	Differences in abscission loss			Differences in insect damage			Differences in possum damage		
	Feb-May	Aug-Nov	Nov-Feb	Feb-May	Aug-Nov	Nov-Feb	Feb-May	Aug-Nov	Nov-Feb
A. flavida, Craigieburn	O	O	O	--	--	N	N	--	--
A. flavida, Eglinton	N	--	O	--	N	--	N	N	n/a
P. colensoi, Eglinton	O	O	O	N	N	N	N	--	N
P. colensoi, Waipori	O	O	O	--	--	N	N	n/a	N
P. tetrapetala, Craigieburn	O	O	O	--	--	N	n/a	n/a	N
P. tetrapetala, Ohau	O	O	O	N	N	N	n/a	n/a	n/a

5.2.2.5. Effect of insect galls on leaf abscission

Insect galls had no significant effect on leaf abscission in either *P. tetrapetala* population (Table 5.5). All *P. tetrapetala* plants had at least some insect galls on their leaves, but plants were unevenly infected; some plants had multiple galls on nearly every leaf, while others had few affected leaves. Galls appeared on leaves within several weeks of leaf emergence, but they were abundant on old leaves as well.

Table 5.5. Results of Chi-square tests comparing number of galls between leaves that did and did not abscise between February 1997 and February 1998.

Species/site	No. galls	No. leaves not abscised	No. leaves abscised (% abscised)	Overall Chi-square	p-value
P. tetrapetala, Craigieburn	0	2124	300 (12.4)	3.36	0.3395
	1	512	55 (9.7)		
	2	165	20 (10.8)		
	3- 6	115	15 (11.5)		
P. tetrapetala, Ohau	0	1659	427 (20.5)	4.62	0.2020
	1	230	71 (23.6)		
	2	70	20 (22.2)		
	3-6	42	5 (10.6)		

5.2.2.6. Effect of leaf damage on leaf abscission

Damaged leaves were significantly more likely to abscise than expected and undamaged or lightly damaged leaves were less likely to abscise than expected in 20 of the 24 Chi-square tests (Tables 5.6.a, b, c, and d). In two cases (*P. tetrapetala* at Lake Ohau between May- August and *A. flavida* at Eglinton between August and November), undamaged leaves were significantly more likely to abscise than damaged leaves. In the two cases that were not significant (*P. tetrapetala* at Craigieburn between May- August and *A. flavida* at Eglinton between November- February), plants had very low abscission rates and few severely damaged leaves, and thus, a comparison could only be made between damaged and undamaged leaves.

Table 5.6.a. Chi-square test results of the effect of previous damage on leaf abscission, February- May 1997.

Species/site	Previous damage (% leaf gone)	No. leaves not abscised	No. leaves abscised (% abscised)	Overall Chi-square	p-value
A. flavida, Craigieburn	0	2974	128 (4.1)	28.02	0.0000
	12.5	357	23 (6.1)		
	38	174	17 (8.9)		
	63- 87.5	54	10 (15.6)		
A. flavida, Eglinton	0	699	705 (50.2)	164.29	0.0000
	12.5	171	160 (48.3)		
	38	96	79 (45.1)		
	63	12	20 (62.5)		
	87.5	9	199 (95.7)		
P. colensoi, Eglinton	0	909	79 (8.0)	39.01	0.0000
	12.5	344	61 (15.1)		
	38	157	35 (18.2)		
	63- 87.5	56	19 (25.3)		
P. colensoi, Waipori	0	1426	43 (2.9)	14.79	0.0006
	12.5	531	31 (5.5)		
	38- 87.5	104	10 (8.8)		
P. tetrapetala, Craigieburn	0	2806	50 (1.8)	15.65	0.0004
	12.5	260	5 (1.9)		
	38- 87.5	174	11 (5.9)		
P. tetrapetala, Lake Ohau	0	2739	64 (2.3)	6.30	0.0428
	12.5	340	11 (3.1)		
	38- 87.5	139	8 (5.4)		

Table 5.6.b. Chi-square test results of the effect of previous damage on leaf abscission, May- August 1997.

Species/site	Previous damage (% leaf gone)	No. leaves not abscised	No. leaves abscised (% abscised)	Overall Chi-square	p-value
A. flavida, Craigieburn	0	2831	122 (4.1)	20.13	0.0002
	12.5	351	15 (4.1)		
	38	171	7 (3.9)		
	63- 87.5	54	10 (15.6)		
A. flavida, Eglinton	0	259	268 (50.9)	101.56	0.0000
	12.5	70	107 (60.5)		
	38	41	63 (60.6)		
	63- 87.5	12	167 (93.3)		
P. colensoi, Eglinton	0	737	29 (3.8)	61.49	0.0000
	12.5	367	20 (5.2)		
	38	204	18 (8.1)		
	63- 87.5	69	22 (24.2)		
P. colensoi, Waipori	0	1249	105 (7.8)	22.87	0.0000
	12.5	479	65 (11.9)		
	38	93	17 (15.5)		
	63- 87.5	14	6 (30.0)		
P. tetrapetala, Craigieburn	0	2760	54 (1.9)	2.11	0.1462
	12.5- 87.5	423	13 (3.0)		
P. tetrapetala, Lake Ohau	0	2180	73 (3.2)	4.55	0.0329
	12.5- 87.5	434	6 (1.4)		

Table 5.6.c. Chi-square test results of the effect of previous damage on leaf abscission, August- November 1997.

Species/site	Previous damage (% leaf gone)	No. leaves not abscised	No. leaves abscised (% abscised)	Overall Chi-square	p-value
A. flavida, Craigieburn	0	2398	416 (14.8)	20.48	0.0001
	12.5	284	79 (21.8)		
	38	132	40 (23.3)		
	63- 87.5	45	13 (22.4)		
A. flavida, Eglinton	0	18	171 (90.5)	6.82	0.0330
	12.5	7	49 (87.5)		
	38- 87.5	9	27 (75)		
P. colensoi, Eglinton	0	657	33 (4.8)	17.15	0.0007
	12.5	380	21 (5.2)		
	38	181	25 (12.1)		
	63- 87.5	72	8 (10)		
P. colensoi, Waipori	0	1181	36 (3.0)	16.43	0.0003
	12.5	462	33 (6.7)		
	38- 87.5	113	10 (8.1)		
P. tetrapetala, Craigieburn	0	2696	64 (2.3)	10.47	0.0053
	12.5	245	11 (4.3)		
	38- 87.5	162	10 (5.8)		
P. tetrapetala, Lake Ohau	0	2045	72 (3.4)	6.43	0.0401
	12.5	301	17 (5.3)		
	38- 87.5	121	9 (6.9)		

Table 5.6.d. Chi-square test results of the effect of previous damage on leaf abscission, November 1997- February 1998.

Species/site	Previous damage (% leaf gone)	No. leaves not abscised	No leaves abscised (% abscised)	Overall Chi-square	p-value
A. flavida, Craigieburn	0	1747	634 (26.6)	13.90	0.0030
	12.5	202	94 (31.8)		
	38	105	28 (21.1)		
	63- 87.5	34	26 (43.3)		
A. flavida, Eglinton	0	417	73 (14.9)	0.01	0.9147
	12.5- 87.5	36	6 (14.3)		
P. colensoi, Eglinton	0	1087	183 (14.4)	14.50	0.0059
	12.5	353	52 (12.8)		
	38	168	31 (15.6)		
	63	54	13 (19.4)		
	87.5	6	6 (50)		
P. colensoi, Waipori	0	2053	132 (6.0)	13.45	0.0038
	12.5	425	31 (6.8)		
	38	87	12 (12.1)		
	63- 87.5	20	5 (20)		
P. tetrapetala, Craigieburn	0	2544	151 (5.6)	24.08	0.0000
	12.5	242	11 (4.3)		
	38	129	8 (5.8)		
	63- 87.5	18	7 (28)		
P. tetrapetala, Lake Ohau	0	2613	312 (10.7)	27.54	0.0000
	12.5	273	50 (15.5)		
	38	83	13 (13.5)		
	63- 87.5	21	12 (36.4)		

Table 5.7 summarises the results of the Chi-square tests for the effects of previous leaf damage on leaf abscission during the four seasons monitored February 1997 to February 1998. Only two populations during one season each did not experience significantly more abscission on leaves that were damaged than on undamaged leaves.

Table 5.7. Results of Chi-square tests between previous leaf damage and leaf abscission on each population during each season from Feb. 1997 to Feb. 1998. A + signifies a positive relationship, a – signifies a negative relationship, and a 0 represents a non-significant relationship.

Species/site	**Previous damage v. abscission**			
	Feb-May	**May-Aug**	**Aug-Nov**	**Nov-Feb**
A. flavida, Craigieburn	+	+	+	+
A. flavida, Eglinton	+	+	–	0
P. colensoi, Eglinton	+	+	+	+
P. colensoi, Waipori	+	+	+	+
P. tetrapetala, Craigieburn	+	0	+	+
P. tetrapetala, Ohau	+	–	+	+

5.2.3. Discussion

5.2.3.1. Effects of leaf age

Old leaves were significantly more likely to abscise than young leaves, even after new growth had been present for some time, but new leaves also had very high abscission rates soon after emergence. Mistletoe leaves probably have a normal survivorship curve, where survivorship is low for very new leaves, it increases as leaves age, and then drops again as leaves begin to senesce. The causes of abscission are probably different for new and old leaves. Previous herbivory, insufficient resources for growth, or mechanical damage to softer young tissue (e.g. by branch movement) may result in the loss of a young leaf, while accumulated damage or senescence may lead to abscission of an old leaf.

In contrast, insect damage was significantly higher on young leaves than on old leaves. Insect preference for new foliage was most apparent soon after leaves appeared, and

damage became more uniform as leaves aged. Meads (1976) found that caterpillars preferred new growth on northern rata, while stick insects browsed on foliage of all ages. New leaves on most plants tend to have a higher palatability and nutritive value than mature leaves, which makes them more appealing to a wide range of herbivores (Opler 1978; Payton 1989). On the other hand, senescent leaves may sometimes undergo chemical changes that also make them relatively palatable to insects (Opler 1978).

Possums also strongly preferred young leaves, but unlike insects, possums maintained this preference even as new growth aged. These findings reinforce results from captive possum feeding trials that also showed a strong preference for new foliage (see section 5.5.2.1). Browse on new growth could be particularly detrimental to mistletoes, because these species flower on the previous year's woody growth, and thus two seasons of flowering can be eliminated in one attack (Dopson 1997).

In contrast, Owen (1993) suggested that possums prefer old leaves to new ones, since he recorded possum browse on *Peraxilla colensoi* almost exclusively during the winter (May- August), when young and old leaves were virtually indistinguishable. He suggested that either possums prefer old leaves to new ones, or that fewer alternative food sources were available during the winter (Owen and Norton 1995). However, Owen (1993) did not track leaf loss on all plants between November and February. Patterns of browse on previous growth appeared to show preference for older leaves, but browse patterns can be difficult to interpret as leaves age, particularly since many damaged leaves may abscise (see section 5.2.2.6).

Furthermore, Owen and Norton (1995) found that *P. colensoi* was most abundant in the possum diet in November, and possums also had seasonal preferences for new shoots of other species. Numerous authors have also shown that possums prefer seral species with short-lived or deciduous leaves and fewer chemical defences (e.g. Proctor-Gray 1984; Cates and Orians 1975). Most generalist arboreal folivores feed almost exclusively on newly produced leaves that have low levels of allelochemicals, while only specialists usually feed on mature and senescent leaves (Opler 1978).

Owen's (1993) results do, however, suggest that we should be cautious in making generalisations about possum preferences from any short-term study. Although I

consistently observed possum browse on new growth, it is possible that possums preferentially browse on old growth in certain cases. For example, senescent leaves may contain lower levels of toxins than mature leaves, which to some herbivores could outweigh the disadvantage of their lower nutritional value (Opler 1978).

The amount of previous damage on each leaf could have confounded the effects of leaf age, because damaged leaves have less area available for loss during the following time periods. However, this is unlikely to have posed a serious problem because damaged leaves were more likely to abscise than undamaged ones (see 5.2.2.6), and thus leaves with more than 50% of their area removed were uncommon. Leaf age and season are also related factors, since most new leaves for all three species emerge during late spring or summer (October- February). This relationship is discussed in section 5.4.3.1 on seasonal shifts in leaf loss.

5.2.3.2. Effects of galls and previous damage on leaf abscission

The galls on *Peraxilla tetrapetala* leaves are probably caused by the insect *Eriococcus elytranthe*, but insects depart the galls early and thus little is known about these insects (Patrick and Dugdale 1997). Galls do not appear to increase leaf loss, although they could have a physiological effect on plants (e.g. by using plant resources or causing disease). No such impact was observed, though, and plants with numerous galls appeared as healthy as non-infected plants.

In contrast, severely damaged leaves (i.e. more than 50% of the leaf area removed) were significantly more likely to abscise than undamaged or lightly browsed leaves (Table 5.6.a-d). Leaf abscission is a common response to herbivory, because although shedding leaves reduces the overall photosynthetic capacity of a plant, it may benefit a plant overall by reducing microbial infection and preventing the depression of transpiration and photosynthesis in undamaged tissue (Addicott 1982). Because possums often browsed leaves to their petioles, and these petioles are likely to abscise quickly, high levels of abscission may be associated with possum defoliation (see also section 4.4.1.2 on cryptic possum damage). Meads (1976) also observed that northern rata trees dropped browsed leaves earlier than undamaged leaves, and defoliation usually followed heavy browsing episodes.

5.3. VARIATION BETWEEN BRANCHES

5.3.1. Methods

At the branch level, I examined how branch position within a plant affected leaf loss. In particular, past observations suggested that plants might suffer more possum damage on branches that were most accessible (e.g. top and bottom branches that could be bent toward the browsing animal), while insect browse would tend to be more evenly spread across a plant (see below). Branch positions were recorded as: 1) top third of the plant, 2) centre of the plant, 3) bottom third of the plant, or 4) against the main trunk of the host tree.

Possum and insect leaf loss data at the branch level could not be normalised. Thus, a Kruskall-Wallace analysis of variance test was used to compare the combined data for all six populations over all four monitoring periods. Sample sizes for branch positions and branches with possum browse were too small to analyse data per population. In addition, Chi-square tests were used to compare the number of branches in each position that suffered either possum or insect damage. Only the Eglinton *Alepis flavida* population sustained enough possum browse to derive meaningful results from this test.

5.3.2. Results

Observationally, most possum browse appeared to occur on branches near the tops of plants or near the host trunk. Often, discrete sections of a plant were browsed, and rebrowse was often recorded on these same sections. Areas of browse usually corresponded to what appeared to be the easiest branches for possums to reach. The most obvious examples were several *Peraxilla colensoi* plants at Waipori that were located far out on an isolated host tree branch. Some of the mistletoe branches could not be reached from the host branch, but the branches that could have been bent toward the animal showed clear signs of heavy browse.

In contrast, a Kruskall-Wallace analysis of variance test showed no significant effect of branch position on possum damage, insect damage, or leaf abscission (Table 5.8). When the small number of branches with the "against host trunk" branch position were excluded, the three tests were still not significant, although the effect on possum loss was nearly significant ($F=2.71$, $p=0.0648$). Branches against the host trunk had the

highest mean loss from possums, followed by branches on the top of plants, and then branches in the centre of plants. Branches at the bottom of plants had the lowest mean possum loss.

Alepis flavida at Eglinton was the only population that had enough branches with possum browse to conduct Chi-square tests. Branches with the "against host trunk" branch position again had to be excluded because of the small sample size. The tests showed no significant effects of branch position on either insect browse (Chi-square=3.96, d.f.=2, p=0.1383) or possum browse (Chi-square=3.61, d.f.=2, p=0.1643) over all time periods in this population.

Table 5.8. Effect of branch position on leaf loss on all branches, Feb. 1997- Feb. 1998, and results of Kruskall-Wallace analysis of variance tests.

Branch position	Sample size (branches per season)	Mean % abscission	Mean % insect loss	Mean % possum loss
top	572	11.78	0.78	0.67
centre	1007	11.86	0.64	0.50
bottom	576	10.25	0.78	0.22
against host trunk	37	13.81	0.74	1.41
F-value		0.59	1.12	2.13
p-value		0.6260	0.3382	0.0927

5.3.3. Discussion

Although the position of a branch had no statistical effect on leaf damage, both observations and the general pattern of mean possum loss suggests that possums tended to browse top branches and branches close to the trunk. Possums might prefer branches at the top and close to the trunk for several reasons. First, new shoots often grow up from the top of plants, and possums prefer these young leaves (see section 5.2.3.1). In addition, these branches might be easiest to reach, particularly if they could be bent for easy access from major host branches.

On the other hand, our impressions of what is "accessible" to possums may be misleading. For example, *Alepis flavida* usually occurs far out on thin branches that do

not seem capable of supporting the weight of a possum (Powell and Norton 1994), but possums browsed this species most heavily (see Table 4.5). Moreover, branch position is probably irrelevant to browse on *A. flavida*, because plants have long limbs and few orders of branching (Powell and Norton 1994).

The statistical methods used in this case may be insensitive to effects of branch position, because differences between populations and seasons could not be eliminated. However, each population had a sample size of 100 branches, which should have improved the power of this test. An additional problem was that branches could not always be chosen to equally represent each "position" category, as the tops of plants were often difficult to reach and plants were irregularly shaped.

Furthermore, the spatial pattern of browse on marked branches often did not accurately reflect browse patterns on the entire plant, especially on large plants. For example, some plants were browsed by possums over an entire section (e.g. top shoots), but this browse may have occurred on only one marked branch, which happened to be at the edge of the section and was thus classified as "centre." Possums do appear to attack distinct sections of a plant rather than spreading damage over the entire plant (unless the plant is small and can be defoliated; see section 4.4.2), but this behaviour is probably dependent on multiple factors related to the accessibility and palatability of plant foliage.

5.4. VARIATION BETWEEN PLANTS

5.4.1. Methods

5.4.1.1. Effects of season and plant location

Leaf loss due to abscission, insects, and possums over the four monitoring periods were compared to examine seasonal changes. Plants in the interior of the forest were compared to plants on the forest edge to examine the influence of plant location on leaf loss.

Mean leaf losses from abscission for plants were normalised with a square root transformation, as were insect losses for three populations: *Peraxilla colensoi* at

Eglinton and Waipori and *Peraxilla tetrapetala* at Ohau. These data were then analysed on S-Plus using a multiple factor analysis of variance with season and plant location as predictors. The interaction between season and location was also examined.

Data for insect damage on the remaining three populations (both *A. flavida* populations and *P. tetrapetala* at Craigieburn) and possum damage on all populations could not be normalised because of the numerous zeros (i.e. no browse on the entire plant during that time). Plants were thus classified as either browsed or unbrowsed and then analysed using a binomial GLM model on S-Plus with season and plant location as predictors. Separate tests were conducted for insect browse and possum browse for each population, and the interaction between season and plant location was again tested.

In addition, a Chi-square test was used to test whether plant location affected branch loss (due to possums, wind snow, etc.) during the year on *P. tetrapetala* at Lake Ohau. *A. flavida* at Eglinton was the only other population that had multiple branches lost, but all ten plants were located on the edge of the forest (see section 4.3.1).

5.4.1.2. Effects of plant volume and height

Plant volume and height off the ground were measured each time leaf loss was monitored. Volume was estimated by multiplying plant height from bottom branch to top, length North/South, and length East/West. The effects of plant height and volume on total mean leaf loss were analysed using an analysis of variance test on S-Plus, with volume, height, and season as predictors. Total leaf loss was normalised with a square root transformation. Separate tests were conducted for each population, and the interactions between each of the predictors were also tested.

5.4.2. Results

5.4.2.1. Effects of season and plant location on abscission rates

Leaf loss from abscission varied significantly with season for both *P. tetrapetala* populations and both *A. flavida* populations, but not for either *P. colensoi* population (Table 5.9; see also Table A2 in Appendix 1). Abscission losses were greatest between November and February for both *P. tetrapetala* populations, as well as for the *A. flavida*

population at Craigieburn. In contrast, *A. flavida* at Eglinton experienced the most abscission between February and May, and abscission consistently declined over the ensuing seasons.

Table 5.9. Effect of season on leaf loss from abscission and results of analysis of variance tests.

Species/site	Season	Mean % leaf loss from abscission	F-value	Pr(F)
A. flavida, Craigieburn	Feb-May	4.44	35.53	0.0000
	May-Aug	4.26		
	Aug-Nov	16.65		
	Nov-Feb	19.24		
A. flavida, Eglinton	Feb-May	52.42	12.62	0.0011
	May-Aug	47.56		
	Aug-Nov	31.27		
	Nov-Feb	8.59		
P. colensoi, Eglinton	Feb-May	11.24	0.16	0.6921
	May-Aug	5.40		
	Aug-Nov	4.45		
	Nov-Feb	12.95		
P. colensoi, Waipori	Feb-May	3.85	0.03	0.8738
	May-Aug	8.88		
	Aug-Nov	2.48		
	Nov-Feb	5.72		
P. tetrapetala, Craigieburn	Feb-May	1.93	6.71	0.0137
	May-Aug	2.08		
	Aug-Nov	2.61		
	Nov-Feb	3.42		
P. tetrapetala, Ohau	Feb-May	2.28	6.57	0.0147
	May-Aug	2.22		
	Aug-Nov	2.05		
	Nov-Feb	8.39		

The effect of plant location could not be tested on *A. flavida* plants at Eglinton, because all of the monitored plants were located on the forest edge. In the remaining populations, plants on the edge did not have significantly different abscission rates than plants located in the forest interior (Table 5.10; see also Table A2 in Appendix 1). The interaction between season and plant location was also not significant at any site.

Table 5.10. Effect of plant location on leaf abscission and results of analysis of variance tests.

Species/site	No. plants in each location		Mean % leaf loss from abscission	F-value	Pr(F)
A. flavida, Craigieburn	edge	5	10.69	0.49	0.4888
	interior	5	11.61		
A. flavida, Eglinton	edge	10	34,96	N/A	N/A
	interior	0	N/A		
P. colensoi, Eglinton	edge	9	8.77	1.38	0.2474
	interior	1	6.13		
P. colensoi, Waipori	edge	6	5.87	1.30	0.2622
	interior	4	4.29		
P. tetrapetala, Craigieburn	edge	3	2.81	0.87	0.3564
	interior	7	2.38		
P. tetrapetala, Ohau	edge	4	2.59	0.52	0.4736
	interior	6	3.16		

In addition, the number of tagged branches that were lost during the year on *P. tetrapetala* at Lake Ohau did not significantly differ between edge and interior plants (Chi-square=1.14, df=1, p=0.2859). The four edge plants possessed 7 of the 23 branches (30.4%) that were lost at this site.

5.4.2.2. Effects of season and plant location on insect damage

Three populations experienced seasonal variation in insect damage: *P. colensoi* at Waipori, *A. flavida* at Eglinton, and *P. tetrapetala* at Craigieburn (Table 5.11; see also Table A3 in Appendix 1). All three groups had significantly more insect damage between November and February than during the other seasons.

Table 5.11. Effect of season on insect damage and results of analysis of variance and Chi-square tests. F-values tested differences in mean loss, while deviance tested the number of plants browsed/unbrowsed. The data used for testing significance in each population are in bold.

Species/site	Season	Mean % insect loss	No. plants browsed/ total	F-value or Deviance	Pr(F) or Pr(Chi)
A. flavida, Craigieburn	Feb.- May	0.07	**8/10**	Dev= 2.39	0.1221
	May- Aug	0.04	**5/10**		
	Aug- Nov	0.06	**8/10**		
	Nov- Feb	0.74	**10/10**		
A. flavida, Eglinton	Feb.- May	0.32	**5/10**	Dev= 5.23	0.0222
	May- Aug	0.09	**1/9**		
	Aug- Nov	0.54	**4/9**		
	Nov- Feb	1.24	**9/9**		
P. colensoi, Eglinton	Feb.- May	**3.41**	10/10	F= 0.03	0.8643
	May- Aug	**1.06**	10/10		
	Aug- Nov	**0.75**	10/10		
	Nov- Feb	**3.61**	10/10		
P. colensoi, Waipori	Feb.- May	**0.51**	9/10	F= 7.68	0.0088
	May- Aug	**0.33**	7/10		
	Aug- Nov	**0.45**	8/10		
	Nov- Feb	**1.69**	9/9		
P. tetrapetala, Craigieburn	Feb.- May	0.02	**1/10**	Dev= 19.61	0.0000
	May- Aug	0.03	**3/10**		
	Aug- Nov	0.04	**5/10**		
	Nov- Feb	0.51	**10/10**		
P. tetrapetala, Ohau	Feb.- May	**0.52**	10/10	F= 0.27	0.6081
	May- Aug	**0.16**	9/10		
	Aug- Nov	**0.26**	9/10		
	Nov- Feb	**0.46**	9/10		

Plant location only had a significant effect on *P. tetrapetala* at Craigieburn, where insect damage was greater on the three edge plants than on the seven interior plants (Table 5.12; see also Table A3 in Appendix 1). However, the unequal sample sizes may have skewed results, and location in this test explained less than 10% of the overall deviance, while season explained 35% of the total deviance. The interaction between season and plant location had no effect on any population.

Table 5.12. Effect of plant location on insect damage and results of analysis of co-variance and Chi-square tests. F-values tested differences in mean loss, while deviance tested the number of plants browsed/unbrowsed. The data used for testing significance in each population are in bold.

Species/site	Plant location (no. plants)	Mean % insect loss	No. plants per season browsed/ total (%)	F-value or Deviance	Pr(F) or Pr(Chi)
A. flavida, Craigieburn	edge (5) interior (5)	0.23 0.23	**15/20 (75.0)** **16/20 (80.0)**	Dev= 0.15	0.6960
A. flavida, Eglinton	edge (10) interior (0)	0.55 n/a	19/37 (51.4) n/a	n/a	n/a
P. colensoi, Eglinton	edge (9) interior (1)	**2.32** **1.20**	36/36 (100) 4/4 (100)	F= 2.32	0.1368
P. colensoi, Waipori	edge (6) interior (4)	**0.88** **0.54**	21/24 (87.5) 12/15 (80.0)	F= 1.17	0.2874
P. tetrapetala, Craigieburn	edge (3) interior (7)	0.24 0.11	**8/12 (66.7)** **11/28 (39.3)**	Dev= 4.71	0.0300
P. tetrapetala, Ohau	edge (4) interior (6)	**0.42** **0.32**	15/16 (93.8) 22/24 (91.7)	F= 0.67	0.4195

5.4.2.3. Effects of season and plant location on possum damage

Peraxilla tetrapetala at Lake Ohau experienced no possum browse during this study and was thus omitted from this analysis. Possum browse was rare at all sites, and of 40 cases for each population (ten plants during four seasons), sample sizes for plants with possum browse ranged from just two to nine. Only *Alepis flavida* at Eglinton showed seasonal variation in possum browse, with seven plants receiving possum damage between February and May (Table 5.13; see also Table A4 in Appendix 1). Two of these plants were also browsed between August and November.

Table 5.13. Effect of season on possum damage and results of Chi-square tests. Test results (deviance, p-value) indicate differences in the number of plants browsed. Mean loss is given for information only.

Species/site	Season	Mean % possum loss	No. plants browsed/ total	Deviance	Pr(Chi)
A. flavida, Craigieburn	Feb.- May	0.29	1/10	0.05	0.8306
	May- Aug	0.14	2/10		
	Aug- Nov	0.39	1/10		
	Nov- Feb	0.03	1/10		
A. flavida, Eglinton	Feb.- May	6.78	7/10	12.62	0.0004
	May- Aug	0	0/9		
	Aug- Nov	0.29	2/9		
	Nov- Feb	0	0/9		
P. colensoi, Eglinton	Feb.- May	0.54	2/10	0.63	0.4257
	May- Aug	0	0/10		
	Aug- Nov	0.09	2/10		
	Nov- Feb	0.09	1/10		
P. colensoi, Waipori	Feb.- May	0.54	1/10	0	1.0
	May- Aug	0.33	3/10		
	Aug- Nov	0	0/10		
	Nov- Feb	0.42	2/9		
P. tetrapetala, Craigieburn	Feb.- May	0.03	1/10	0	0.9999
	May- Aug	0	0/10		
	Aug- Nov	0	0/10		
	Nov- Feb	0.99	1/10		

Plant location had a significant effect on possum damage on *A. flavida* at Craigieburn and *P. colensoi* at Waipori (Table 5.14). In both cases, possum browse was only recorded on plants located along the forest edge. However, at both sites, plant location explained less than 5% of the total deviance. *P. colensoi* at Eglinton also only had browse on edge plants, but the browse was not significantly different from zero. The interaction between season and plant location was significant for *P. tetrapetala* at Craigieburn, but only two cases of possum browse were compared (see Table A4, Appendix 1).

Table 5.14. Effect of plant location on possum damage and results of Chi-square tests. Test results (deviance, p-value) indicate differences in the number of plants browsed. Mean loss is given for information only.

Species/site	Plant location (no. plants)	Mean % possum loss	No. plants per season browsed/ total (%)	Deviance	Pr(Chi)
A. flavida, Craigieburn	edge (5) interior (5)	0.43 0	5/20 (25.0) 0/20 (0)	7.66	0.0057
A. flavida, Eglinton	edge (10) interior (0)	1.77 n/a	9/37 (24.3) n/a	n/a	n/a
P. colensoi, Eglinton	edge (9) interior (1)	0.20 0	6/36 (16.7) 0/4 (0)	1.39	0.2387
P. colensoi, Waipori	edge (6) interior (4)	0.54 0	6/24 (25.0) 0/15 (0)	6.82	0.0090
P. tetrapetala, Craigieburn	edge (3) interior (7)	0.03 0.35	1/12 (8.3) 1/28 (3.6)	0.37	0.5436

5.4.2.4. Summary of effects of season and plant location

Table 5.15 summarises the effects of season and plant location (edge or interior of the forest) on mean leaf loss from abscission, insects, and possums. Significantly more abscission occurred from August-November than during other seasons in three populations, while insect damage was significantly greater from November-February than during other seasons for three populations. Possum damage did not significantly differ between seasons for most populations. Edge effects did not significantly alter leaf loss rates in most populations.

Table 5.15. Summary of effects of season and plant location on leaf loss due to abscission, insects, and possums in each population from Feb. 1997 to Feb. 1998. Significant seasonal effects are denoted with the number of the season during which leaf loss was greatest (1=Feb-May, 2=May-Aug, 3=Aug-Nov, 4=Nov-Feb). Significant effects of location are denoted by E if edge plants had significantly more loss than interior plants, or I if vice versa.

Species/site	Effects of season on			Effects of plant location on		
	Abs.	Ins.	Pos.	Abs.	Ins.	Pos.
A. flavida, Craigieburn	3	--	--	--	--	E
A. flavida, Eglinton	2	4	1	n/a	n/a	n/a
P. colensoi, Eglinton	--	--	--	--	--	--
P. colensoi, Waipori	--	4	--	--	--	E
P. tetrapetala, Craigieburn	3	4	--	--	E	--
P. tetrapetala, Ohau	3	--	n/a	--	--	n/a

5.4.2.5. Effects of plant size and height off the ground

Plant height had no significant effect on total leaf loss in any population (see Table A5, Appendix 1). Plant volume had significant effects only on total leaf loss on *P. colensoi* at Eglinton ($F=5.39$, $p=0.0267$). Figure 5.1 shows that total leaf loss was greater on larger plants. The effect of volume on leaf loss on *P. colensoi* at Waipori was not significant, but the interaction between volume and season was significant ($F=6.54$, $p=0.0163$; see also Table A5, Appendix 1). The relationship between volume and total leaf loss was then tested using a linear regression for each season. Total leaf loss was significantly greater on larger plants from May-August (Figure 5.2; $F=5.81$, $p=0.0424$). *P. colensoi* plants were on average larger (range= 0.29- 46.66 m^3, mean= 8.24 m^3) than both *A. flavida* (range= 0.19- 2.73 m^3, mean= 0.90 m^3) and *P. tetrapetala* (range= 0.18- 14.52 m^3, mean= 3.64 m^3).

Figure 5.1. Linear regression between total leaf loss and plant volume for *P. colensoi* at Eglinton during all four seasons (n=40, R^2=0.1430, y = 0.0566x + 2.7669).

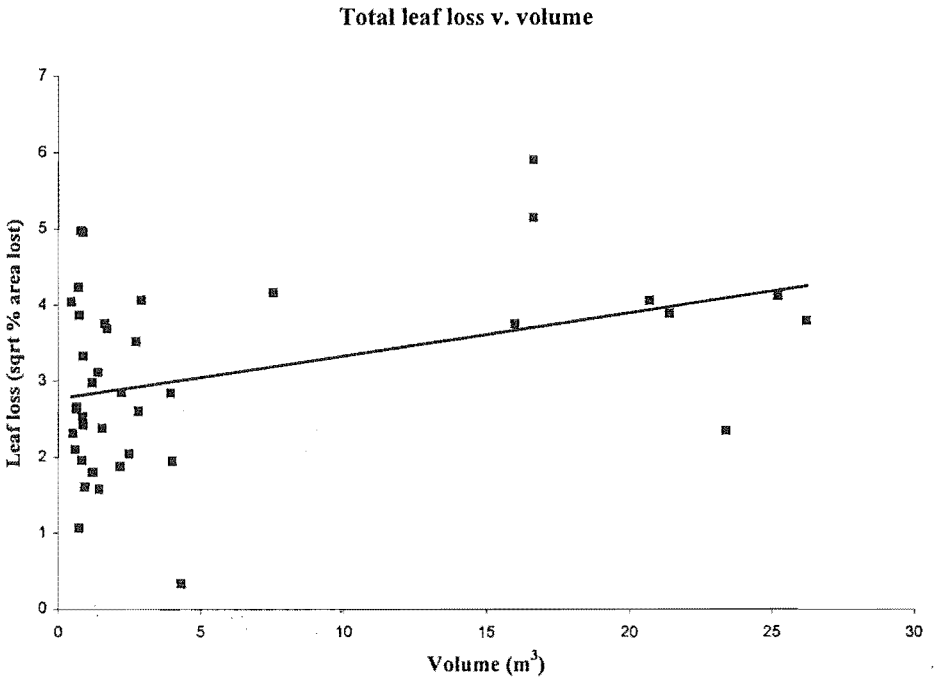
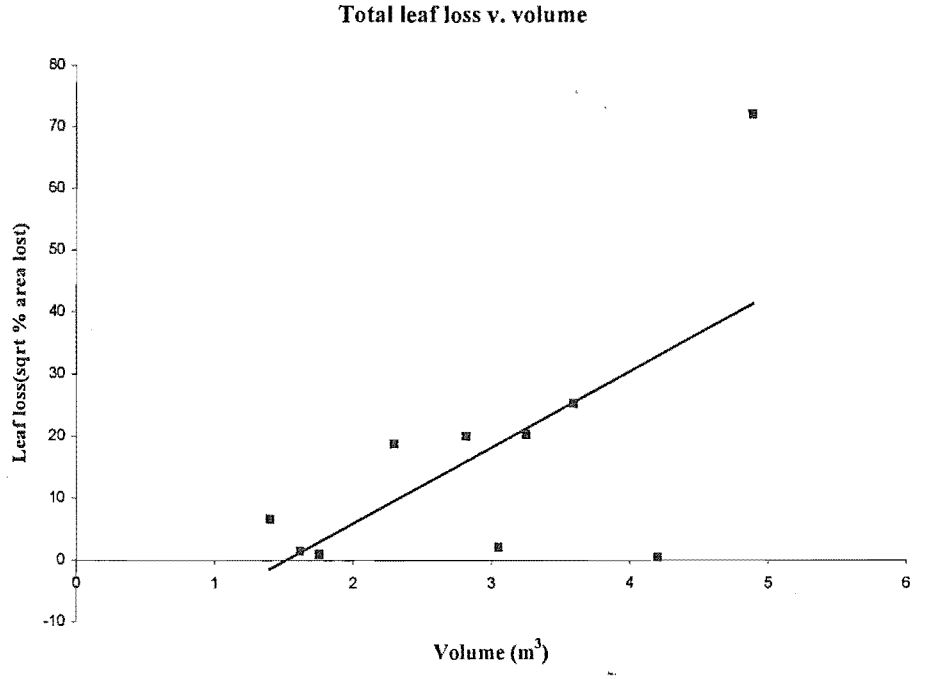


Figure 5.2. Linear regression between total leaf loss and plant volume for *P. colensoi* at Waipori from May-August (n=10, R^2=0.4208, y = 12.238x – 18.572).



5.4.3. Discussion

5.4.3.1. Seasonal variation in leaf loss

Seasonal shifts in leaf loss from abscission may either be due to environmental factors (e.g. changes in light, temperature, or moisture) or to changes in the ratio of young to old leaves, since most new leaves for the three mistletoe species emerge during late spring or summer (October- February). *Peraxilla tetrapetala* and *Alepis flavida* at Craigieburn had the most leaf abscission during summer (November- February), possibly because new growth either diverted resources away from old leaves, or because newly emerged leaves had higher abscission rates than other leaves (see section 5.2.2.1). Alternatively, changes in light or temperature could have induced leaf abscission.

Peraxilla colensoi did not show any seasonal trend in abscission of leaves. Perhaps because this species has larger leaves that require more resources for their production and maintenance, leaf loss is spread more consistently over the entire year. New Zealand plant species have developed the evergreen habit to various degrees, and both the extent of periodicity and the peak time of leaf-fall may vary between congeneric species and between sites for the same species (e.g. *Nothofagus* spp.; Wardle 1984).

Seasonal changes in herbivory could be caused by changing food availability, seasonal nutritional requirements, changes in plant toxin and nutrition levels (e.g. a change in the ratio of new to old leaves), or changes in herbivore numbers. Insect damage was significantly higher between November and February than during other seasons in three mistletoe populations, possibly because insects preferred the newly emerging foliage abundant during this season (see section 5.2.2.2). In addition, insect larvae may require the most food during the season prior to moth emergence (see Table 4.1). However, it is not clear why only one population of each species experienced this seasonal effect.

The *A. flavida* population at Eglinton experienced unique circumstances that may explain trends in this population. *A. flavida* at Eglinton deviated from most typical patterns of leaf loss associated with season, and plants had unusually high abscission rates from February until November, with highest losses between February and May (see Table 4.4). These plants were also heavily browsed by possums during these months, and once possum control operations were initiated in November, possum browse ceased and abscission rates dropped significantly (see Table 4.4). Thus, much

of the abscission on these plants may have been secondary possum damage (see section 4.4.1.2), which probably masked the effect of leaf age on abscission (see section 5.2.2.1) and suggested a non-existent seasonal preference (Table 5.9). Possums probably began browsing plants during the summer and decreased browsing only as plants lost leaves and the possum population declined.

For the remaining five mistletoe populations, possum damage was not seasonal (Table 5.1.3). The heaviest browse might have been expected during summer because possums preferred new shoots (see section 5.2.3.1 and 5.5.3.1). On the other hand, Pekelharing *et al.* (1998a) suggested that the effects of possums on native forest plants are greatest during the winter and early spring, because other food sources (e.g. introduced grasses and herbs in nearby clearings) are not available. Numerous studies have confirmed that possums usually shift their diets seasonally, but these changes may vary considerably from one site to the next. In the Tongariro-Taupo area, possums browse mistletoes during the autumn, when plants have fruits and/or new shoots (Jones 1997b). However, Owen (1993) recorded possum browse on *P. colensoi* almost exclusively during the winter (May to August), possibly because fewer alternative food sources were available to possums during this season (Owen and Norton 1995). Simpson (1997) also reported that possums browsed *P. tetrapetala* in the Dingle Valley between May and September, when the possum's main food source, tussocks, were covered in snow. Obviously, seasonal patterns in possum browse on mistletoe are site-specific, depending on the distribution and abundance of plant species in the area, local climate, and plant and herbivore population densities. However, consistent seasonal preferences may also not be obvious from studies to date because possum browse is patchy and only a few studies with relatively small sample sizes have investigated seasonal trends in browse on mistletoe.

The season during which possums browse mistletoes could alter the consequences for plant health (Danell *et al.* 1994). Payton (1985) showed that southern rata branches died when they were defoliated during their growth period, but when defoliation occurred after the growth period, twigs produced new leaves from over-wintering buds. Thus, the retention of leaves following bud break may be critical, at least for certain species, to allow the build-up of sufficient carbohydrate reserves (Payton 1985). Repeated leaf-stripping during summer could therefore have much more detrimental effects than browsing during the winter.

5.4.3.2. Effect of plant location

The location of mistletoe plants in this study did not appear to affect leaf loss. I hypothesised that plants on the edge of the forest were more susceptible to damage from wind, snow, and drought, but no such effects were apparent. In fact, wind and snow break appeared to have the largest effect on *Peraxilla tetrapetala* at Lake Ohau, where interior plants had higher abscission rates than exterior plants. Furthermore, edge plants did not have significantly greater branch loss than interior plants. I observed plants on the lake shore that appeared to be suffering from exposure, but these plants also usually had small, tough leaves and a highly branched architecture, which might have made them more resistant to heavy winds and snow damage. Also, the Ohau forest remnant has numerous internal "edges," where old trees have fallen or paths have been worn. Thus, interior plants at Ohau may have been more exposed than plants within other, less disturbed forest fragments.

Insect damage on *P. tetrapetala* at Craigieburn was significantly higher on edge plants than on interior plants, but only three edge plants were compared to seven interior plants and the deviance from this effect accounted for only a small proportion of the overall residual deviance. Two populations had possum browse only on edge plants (*A. flavida* at Craigieburn and *P. colensoi* at Waipori), but again, the effects accounted for less than 5% of the total deviance. Possums have been shown to prefer forest/pasture margins, where both den sites and food are abundant (Coleman *et al.* 1980; Coleman *et al.* 1985), and thus, edge plants might be expected to be more susceptible. However, these results probably cannot be extrapolated to generalise about possum behaviour because of the very small sample sizes.

5.4.3.3. Effects of plant height and size

The height of plants off the ground did not appear to affect leaf loss on mistletoes in this study. However, monitored plants only represented a limited range of heights that could be reached easily with a step ladder. Mistletoes growing higher in host trees might be browsed more frequently, because possums are arboreal and often sleep high in trees. On the other hand, high plants may be more exposed to rain and wind, which could deter possums, especially at higher altitude or latitude (i.e. colder) sites. No quantitative

studies have investigated the effect of possums on mistletoes close to the canopy, because they are so difficult to monitor. The Department of Conservation attempts to monitor plants at various heights, but leaf loss on high plants usually cannot definitively be attributed to possums because plants are so difficult to see (Jones 1997a; C. Rance, personal communication).Effects of height may also vary for the three mistletoe species, because *P. colensoi* plants are usually located in the mid to upper canopy, while *A. flavida* and *P. tetrapetala* are more common in the low to middle height range of host trees (Norton *et al.* 1997).

In contrast, a wide range of plant sizes were monitored, and both populations of *P. colensoi* showed some effect of volume on total leaf loss. *P. colensoi* is the largest of the three beech mistletoe species, and in this study, these plants were on average much larger than plants of the other two species (see Chapter 2 and section 5.4.2.5). It is unclear why larger plants would lose more leaves than smaller plants, unless large plants are also older and beginning to senesce. Alternatively, possums may prefer large plants because if they move at random, they are more likely to encounter large plants, or because large plants offer a larger quantity of food (Milne 1996). Payton (1985, 1988) also found that older and larger southern rata (*Metrosideros umbellata*) trees were more heavily browsed than small, young trees.

5.5. VARIATION BETWEEN SPECIES AND SITES

The purpose of this experiment was to test variations in plant palatability to possums between: 1) old and new mistletoe foliage, 2) individual plants from the same population, 3) plants of the same species from different sites, and 4) plants of different species. Four separate trials were conducted to test each of these hypotheses using captive possums housed at Landcare Lincoln.

5.5.1. Methods

5.5.1.1. Differences between plants within a population

For this trial, six branches approximately 15- 25 cm long were collected from each of four *Peraxilla tetrapetala* plants at Craigieburn on 23 February 1998. The weight and

number of new leaves (summer 1997-98 growth) and old leaves (previous growth) on each branch was recorded, and branches were marked with colour wires to differentiate the four plants. The following day, twelve possums were presented with two mistletoe branches from different individuals, so that two possums received each possible combination of plant pairs. Possums were allowed to feed on the branches for 45 minutes, before all uneaten foliage was removed from the cage. (This time was chosen as a compromise between allowing possums long enough to exhibit feeding selectivity but not long enough to remove all foliage).

The weight and number of leaves (to the nearest quarter of a leaf) remaining on each branch was again recorded, and the percent of foliage eaten by the possum was calculated by subtracting final from initial weights (or leaf numbers) and dividing by the initial value. A control branch was also weighed before and after the study to determine average water weight loss. This loss was small (2%) and thus, disregarded when calculating the weight changes for trial branches. The percent of total leaf number and weight removed were compared for the four plants using a one-way analysis of variance. Results using branch weights and leaf number were similar for all of the palatability trials, so only results for leaf number are presented here. One possum completely shredded both branches, making it impossible to differentiate between foliage from the two individuals, so only eleven trials could be analysed.

5.5.1.2. Regional differences

For the second trial, I collected two branches from each of ten *Peraxilla tetrapetala* plants from the Eglinton Valley on 7 March 1998. On the same day, two branches from each of ten *Peraxilla tetrapetala* plants at Craigieburn were collected. The following day, 20 captive possums at Landcare were presented with one branch from each location. Procedures were then the same as in the first trial, with possums left to feed for 45 minutes. The percent of foliage eaten was compared for the two locations using a paired t-test. However, a paired t-test assumes that the probabilities of leaves being eaten on either branch are independent of each other. Thus, a more appropriate response was calculated as the log of the proportion of the percentage of Craigieburn foliage eaten divided by the percent of Eglinton foliage eaten. The mean response was then divided by the standard error of the mean to calculate the t-statistic.

5.5.1.3. Differences between species

The final two trials tested whether possums had preferences between the two *Peraxilla* species and between *A. flavida* and *P. tetrapetala*. Two branches from 10 *P. colensoi* plants and 10 *P. tetrapetala* plants in the Eglinton Valley were collected on 7 March 1998. (The *P. tetrapetala* plants were the same ones used in the previous trial for regional differences.) On 15 March 1998, two branches were collected from each of 10 *P. tetrapetala* and 10 *A. flavida* plants at Craigieburn. The day after foliage was collected for each trial, 20 captive possums were fed a branch of each of the two species for 30 minutes (possums in this trial ate foliage more rapidly so the trial had to be shortened). The weight and number of leaves on each branch were recorded before and after feeding, as in the previous trials, and results were analysed as above.

In addition, two possums were fed a branch from *P. tetrapetala* and a branch from mountain beech (*Nothofagus solandrii*) from Craigieburn. Leaves on the *Nothofagus* branch were too numerous to count, and thus only branch weights were recorded. Possums were again allowed to feed for 45 minutes, and the post-trial weight of each branch was recorded.

5.5.1.4. Differences between new and old leaves

During the first trial, I observed that possums were heavily feeding on new growth before turning to mature leaves. The amount of new and old foliage on each branch could not be standardised. Thus, in the following trials, I recorded the number of new and old leaves on each branch, so that the amount of new foliage on branches could be tested as a confounding factor. However, new and old foliage were too difficult to distinguish on *A. flavida* by this late in the growing season, so leaf age was not recorded for this species. Thus, the amount of new and old leaves eaten on Eglinton *P. tetrapetala* (from two trials), Craigieburn *P. tetrapetala*, and Eglinton *P. colensoi* were compared by calculating the log of the percentage of new foliage eaten divided by the percentage of old foliage eaten, and then dividing the mean by the standard error of the mean to calculate the t-statistic for each case. Because in this case I was only interested in the proportion of new to old foliage on each branch and not the total amount of damage, I assumed each branch was an independent sample.

5.5.2. Results

5.5.2.1. Differences between new and old leaves

Possums ate significantly more new leaves than old leaves on both *P. tetrapetala* and *P. colensoi* (Table 5.16). When possums were presented with branches of *P. tetrapetala* from Craigieburn and Eglinton, 13 out of 19 (68%) possums preferred new foliage on the Craigieburn branches, while 15 of 19 (79%) preferred new leaves on Eglinton branches. Of the 20 possums presented with branches of *P. tetrapetala* and *P. colensoi* from Eglinton, 15 preferred new foliage on *P. colensoi* and 18 preferred new foliage on *P. tetrapetala.*

Table 5.16. Comparison of percentage of new and old leaves eaten by possums in palatability trials.

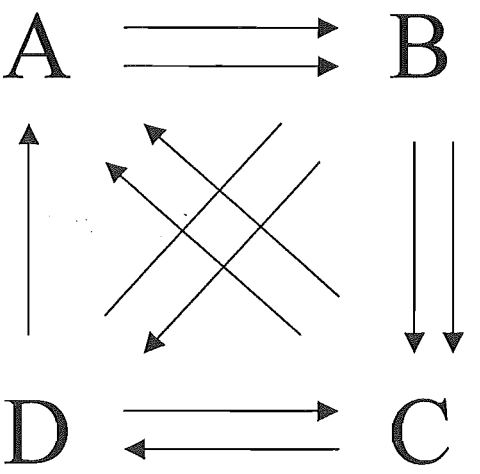
Branches presented	Mean % leaf area eaten	T-statistic	p-value
P. colensoi, Eglinton	new= 33.21 old= 19.38	3.04	0.0067
P. tetrapetala, Eglinton (trial against *P. colensoi*)	new= 46.83 old= 23.98	5.29	0.0000
P. tetrapetala, Craigieburn	new= 46.49 old= 31.52	2.46	0.0237
P. tetrapetala, Eglinton (trial against *P. tetrapetala*, Craigieburn)	new= 61.51 old= 47.83	2.49	0.0221

5.5.2.2. Differences within a population

In the trial that tested for differences in palatability among four *P. tetrapetala* plants at Craigieburn, possums did not consistently prefer certain individuals over others (F=0.68, p=0.5734; Figure 5.3). It was expected that plants with large, fleshy leaves would be more palatable to possums than highly branched plants with small, tough leaves. However, in both this trial and the trial comparing regional differences in *P.*

tetrapetala, possums did not appear to discriminate among branches according to these morphological differences.

Figure 5.3. Possum preferences among four *P. tetrapetala* plants from Craigieburn. Each arrow represents one replicate; one of the A-D replicates was lost (see Methods). Arrows point toward the preferred individual and no arrowhead indicates a tie.



5.5.2.3. Differences between sites and species

Possums did not show a preference for *P. tetrapetala* foliage from either Eglinton or Craigieburn, nor did they have a significant preference for either *Peraxilla* species from Eglinton (Table 5.17). However, possums did highly prefer *A. flavida* over *P. tetrapetala* foliage from Craigieburn plants. Since only two possums were fed *P. tetrapetala* and mountain beech foliage, no statistical analysis was possible. However, in both cases possums ate substantial amounts of mountain beech (37.17% and 51.10%) but more *P. tetrapetala* (63.64% and 77.02% respectively).

Table 5.17. Results of palatability trials comparing plant locations and mistletoe species.

Branches presented	Mean % leaf area eaten	T-statistic	p-value
P. tetrapetala, Craigieburn	37.16	1.899 (df=18)	0.0737
P. tetrapetala, Eglinton	54.88		
P. tetrapetala, Eglinton	37.57	1.81 (df=19)*	0.0863
P. colensoi, Eglinton	26.88		
A. flavida, Craigieburn	80.23	5.56 (df=19)	0.0000
P. tetrapetala, Craigieburn	38.86		

*T-statistic derived from paired t-test in this case; the T-value from the log odds ratio would be even smaller.

5.5.3. Discussion

5.5.3.1. Effects of leaf age on palatability

The palatability trials showed that possums preferentially feed on young leaves before old leaves. These results reinforce observations and data from leaf maps that suggest young leaves are more palatable than mature leaves (see section 5.2.3.1 for a discussion of the effects of leaf age on herbivory).

5.5.3.2. Variation in palatability within populations

Mammalian herbivores commonly discriminate between individuals of a plant species (Lawler *et al.* 1998). Possums have evident preferences for certain plants for reasons that are not at all obvious (e.g. Meads 1976; Fitzgerald 1978; Green 1984; Owen 1993; Milne 1996). Herbivores may discriminate between plants or species partly based on nutrient concentrations (particularly nitrogen), carbon compounds that influence digestion rates, or plant secondary metabolites (Crawley 1983; Bryant *et al.* 1991; Cork and Foley 1991; Ganzhorn 1992; Pastor *et al.* 1997). Even subtle variations in the chemical structure of toxins and deterrents between conspecific individuals can have major effects on their relative palatability (Lawler *et al.* 1998). However, results from this experiment did not indicate that these differences cause possums to consistently choose certain plants over others. Observations also suggest that differential

palatability within a population is not predictable based on morphological features such as degree of branching, or leaf size or "toughness."

It is possible that captive possums simply have different preferences from wild possums, or that the captive animals are less selective than wild ones. However, captive possums have shown strong, repeatable preferences (Edwards 1974; Morgan 1990), and bait lures favoured by captive possums have proven most effective in field trials (Morgan *et al.* 1995). In this experiment, captive possums also showed preferences (e.g. for new leaves and for *Alepis flavida*) that were supported by field evidence.

Instead, possums may base their selection of individuals within a population primarily on factors other than leaf quality and/or taste, although these cannot be ruled out as significant influences given the small sample sizes in this study. Characteristics such as plant accessibility, exposure, location of nearby den sites, and plant location, size, and height (see section 5.4) may also influence possum choices (Payton 1988, Cowan *et al.* 1997b). Because captive possums cannot discriminate between plant foliage based on these characteristics, they may instead simply feed on the first branch they pick up and then move on to the other branch.

Moreover, while these factors may explain why certain plants are initially chosen by possums, behavioural traits may be more important in structuring patterns of damage over time. Possums usually continue to browse the same individuals as long as possible, although they can easily switch to other plants once the preferred sources are depleted (Meads 1976; Green 1984). Because plant productivity usually decreases and chemical defences may increase after herbivory, herbivores should avoid browsed plants, but some studies have shown that herbivores prefer previously browsed individuals (Danell *et al.* 1994). Induced changes in morphology (e.g. an increase in shoot length or increased growth within reach of the herbivore) and positive changes in nutrients may encourage a return to browsed plants (Charnov *et al.* 1976; Danell *et al.* 1994). Powell (1989) found that the complete defoliation of southern rata shoots increased the concentrations of nitrogen, phosphorus, and potassium in leaves the following season. Alternatively, possums may simply opportunistically feed on the first plants they find and return to these plants rather than searching for new individuals. However, given the proximity of browsed and unbrowsed plants (Owen 1993; personal

observation), it seems unlikely that possums are unaware of the individuals that they do not browse.

5.5.3.3. Regional variation in plant palatability

The central paradox of concern to this study was why possums appear to have such a great impact on mistletoes in certain areas (e.g. Mt. Misery) but little or no effect on mistletoes at other sites (e.g. Craigieburn). Other species, such as fuchsia (*Fuchsia excorticata*), also suffer heavy browse at some sites but little damage in other areas despite a long history of possum colonisation (Sweetapple and Nugent in prep), and numerous studies have documented the variation in preferred species between floristically similar areas (e.g. Mason 1958; Fitzgerald 1976; Fitzgerald 1978; Leathwick *et al.* 1983; Coleman *et al.* 1985).

One possibility is that plants from certain regions (provenances) are more palatable than conspecifics from other areas. This variation in palatability could either have a genetic basis or be related to environmental factors (e.g. light, water, or nutrient levels) that alter leaf chemistry and nutrient concentrations. If certain genotypes are in fact more browse resistant, the impact of possums would then be expected to decline over time as the more palatable genotypes are removed from the population (Sweetapple and Nugent in prep.). Alternatively, if differences in palatability reflect site characteristics, then plants at "unpalatable" sites would not be in danger of rapidly deteriorating even if local possum densities increased, while plants at "palatable" sites would continue to be affected even by a small number of possums.

Results from this experiment do not indicate that *P. tetrapetala* plants from the Eglinton Valley are more palatable than Craigieburn plants, despite field observations that *P. tetrapetala* was heavily browsed in the Eglinton Valley prior to possum control operations (C. Rance personal communication), whereas *P. tetrapetala* at Craigieburn has not suffered serious browse for at least five years (J.J. Ladley personal communication). Sweetapple and Nugent (in prep) also found no evidence that provenances of fuchsia with varying browse in the field varied in palatability to captive possums when they were grown in a common garden experiment. Possums seemed to browse the first plant encountered, regardless of provenance, before moving on to the next plant (Sweetapple and Nugent in prep.).

Alternatively, regional differences in possum preferences may result from local changes in nutritional requirements or the availability of alternative food sources (Owen and Norton 1995; Norton 1997). Detailed vegetation surveys were not conducted at my four study sites, but general observations suggest that sites with heavy browse, such as Eglinton, have as many or more alternative food sources as sites with little mistletoe browse, such as Craigieburn. There are significant sections of pasture at both sites, and the Eglinton forest is floristically more diverse and probably contains more palatable understory and shrub species than the relatively simple Craigieburn forest (see section 2.3.1). The area of exotic pine at Craigieburn superficially appears to be the only major food source that is available for possums at Craigieburn but not at Eglinton. However, further vegetation studies are needed to quantify more subtle floral differences that could influence possum diet, particularly since possums may range long distances in search of food (Green and Coleman 1981; Clout and Gaze 1984).

5.5.3.4. Differences in palatability among mistletoe species

In this study, the two *Alepis flavida* populations sustained the most browse during the year (see Table 4.5). In addition, more browse was observed on non-study *A. flavida* plants than on non-study *Peraxilla tetrapetala* at Craigieburn. I also observed several *A. flavida* plants at Lake Ohau that were severely possum browsed, while no browse was recorded on the monitored *P. tetrapetala* at this site.

The feeding trials support these field observations that *A. flavida* is more palatable to possums than *P. tetrapetala*. Possums did not show a preference between the *Peraxilla* species, and thus, *A. flavida* may also be more palatable than *P. colensoi*. Furthermore, *Peraxilla* may not be as highly preferred as once assumed, considering that possums ate almost as much beech foliage as *P. tetrapetala* when branches of the two species were presented together. Possums in the wild will eat *Nothofagus* foliage but it is not considered a preferred species (Wardle 1984; Owen and Norton 1995). Further tests are needed to determine the relative palatability of *Peraxilla* and to determine if possums prefer *A. flavida* to *Peraxilla* foliage from different sites. Even if captive possums do prefer *A. flavida* at different sites, possums still may exhibit different preferences in the field according to local (or seasonal) changes in alternative food sources.

Nonetheless, *A. flavida* was the first species to disappear from many parts of the North Island, presumably because of possum browse (de Lange and Norton 1997, p. 166), although it was probably never common there (de Lange *et al.* 1997a). It is still more abundant than *Peraxilla tetrapetala* in many parts of the South Island, but it may be in danger of rapid decline if it is highly preferred at many sites. Furthermore, *A. flavida* may be more susceptible to repeated browsing than *P. tetrapetala*, because it cannot recover quickly by forming new branches from submerged buds (Powell and Norton 1994; Norton 1997).

5.6. Conclusions

Clearly, numerous factors working in concert determine overall patterns of plant leaf loss. Leaf abscission is the most cryptic part of leaf loss, since it is often difficult to determine unequivocally why leaves have been removed. Old leaves are generally more likely to abscise than new leaves, as are leaves with previous herbivore damage. Abscission is also seasonal for at least two of the mistletoe species (*Alepis flavida* and *Peraxilla tetrapetala*), and large plants may have greater total leaf losses.

Insects and possums can make feeding choices at number of hierarchical levels, all of which influence the consequences of herbivory for mistletoes:

1. *Leaf level*: Both insects and possums prefer new leaves to old ones. In particular, possum preference for young foliage is pronounced throughout the year, as shown by both field data and palatability trials.

2. *Branch level*: Neither insects nor possums consistently browsed leaves according to branch position within a plant. However, possums did appear to choose certain branches or sections of plants, possibly based on relative accessibility and the amount of new growth on the branch. Insects spread browse evenly across branches.

3. *Plant level*: As shown in Chapter 4, possums are very selective of individual plants while insects damage all plants within a population. The factors that influence possum preferences at this level are difficult to determine. Variation in plant height, location within the forest, and palatability did not seem to affect their choices, while plant

volume did have an effect, at least for *Peraxilla colensoi*. Other possible factors that were not tested include plant shape, age (although this may be related to volume), proximity to den sites, exposure, and accessibility. Possum behaviour (Green 1984) and induced changes in nutrient levels or plant morphology (Payton 1989; Danell *et al.* 1994) may also encourage rebrowsing of selected individuals.

4. *Species level*: Palatability trials and field observations indicate that possums prefer *Alepis flavida* to the *Peraxilla* species. Further tests are needed to determine if this preference exists across regions, as the relative palatability of plants to possums generally shifts from one region to another, according to changes in nutritional requirements, local food availability, and environmental conditions.

CHAPTER 6: METHODS OF MONITORING MISTLETOE HEALTH

6.1. INTRODUCTION

In the previous two chapters, I examined the patterns of leaf loss on mistletoes, and suggested how variability in herbivory could influence the consequences of possum and insect damage for plants. In this chapter, I compare various monitoring methods that conservation biologists and managers can use to accurately and efficiently describe these spatial patterns of damage. I begin by discussing the reasons for monitoring mistletoes and the ways that mistletoes have been monitored in the past. I then compare three methodologies that were employed in this study and suggest standard methods for monitoring mistletoes throughout New Zealand.

6.1.1. Appropriate goals and indicators for monitoring

Biodiversity monitoring is "the systematic measurement of variables and processes over time in order to ascertain the degree of deviation from some expected condition" (Hellawell 1991). The important defining characteristic of a monitoring program is the expectation of a defined outcome prior to initiation of the actual monitoring (Norton 1996). Thus, any monitoring program should have clear objectives that can be addressed directly. Norton (1996) identified five key reasons for monitoring biodiversity in New Zealand:

1. to assess trends in individual populations;
2. to assess impacts of introduced species;
3. to assess effectiveness of management actions;
4. to assess changes in community composition and structure; and
5. to assess changes in ecosystem processes.

The overall success of a monitoring program will ultimately depend on how effectively the appropriate questions can be answered using the selected indicator and

methodology. The species or ecosystem attributes that are monitored need to be appropriate for answering the question asked, be sensitive enough to provide the needed information, and be appropriate to the scale of the perturbation of interest (Norton 1996).

Different indicators will obviously be more effective for answering certain questions. For example, ecosystem processes (e.g. litterfall, decomposition, seed dispersal, trophic interactions) may be more useful than individual species as indicators of ecosystem health, while measures of community diversity or species abundance can be used to monitor changes in community structure (O'Donnell 1995; Norton 1996). However, monitoring programs are often designed to answer multiple questions at different hierarchical levels, only some of which are appropriate.

Mistletoe monitoring programs have had diverse goals that correspond to the above general goals of biodiversity monitoring:

1. to assess changes in mistletoe health;
2. to assess the impact of possums on mistletoe health;
3. to assess the effectiveness of possum control operations;
4. to assess changes in plant communities since possum colonisation; and
5. to assess the overall impact of possums on entire beech forest communities.

The first two of these goals are central to most mistletoe monitoring programmes, and they can be directly measured by monitoring individual plants. On the other hand, the last three questions about the broader effects of possums cannot be answered directly with mistletoe data and require the extrapolation of these results to other presumably linked changes in the environment. Owen (1993) suggested that "the apparent sensitivity of mistletoe to possum impacts (Wilson 1984) and its importance within these forest ecosystems...has prompted the Department [of Conservation] to measure the performance of possum control operations by monitoring the condition of mistletoe plants." To make such general assessments, managers must assume that increases in mistletoe health are correlated with decreases in possum densities and increases in the abundance of other native plant species. However, these correlations often do not actually exist, and browse levels on mistletoe do not appear to be predictably related to possum densities (see section 2.3.2). Moreover, possums feed heavily on the most preferred plant species out of proportion to their abundance in the forest (Fitzgerald

1978; Coleman *et al.* 1985; Allen *et al.* 1997), and the relative preferences among these browsed species vary between regions for unknown reasons (e.g. Mason 1958; Fitzgerald 1976; Leathwick *et al.* 1983; Coleman *et al.* 1985). Therefore, possum damage to one species is not predictive of damage to other plant species at any given location, nor is damage to any given species at one location predictive of damage to the same species at other locations.

Thus, mistletoes are probably not appropriate indicators for assessing the "effectiveness" of possum control operations on any factor except for mistletoe health. Thus, rather than using mistletoes as "canaries in a coalmine " to estimate overall possum impacts within a forest, they should only be used to indicate changes in mistletoe health and to warn managers of serious declines in mistletoe population health or structure. Norton (1996) calls this "specialist monitoring," because it is conducted to address specific management questions and has defined applications. With these program goals in mind, a methodology can be developed to provide the most accurate and efficient assessment of possum damage and its consequences for mistletoe health.

6.1.2. History of mistletoe monitoring

The first formal biodiversity monitoring program in New Zealand was conducted in 1897 by Leonard Cockayne, but it was not until the 1940's that monitoring became an integral part of the New Zealand Forest Service policy. Recently, conservation biologists and managers have shown increasing interest in biodiversity monitoring (Norton 1996), and numerous monitoring programs have been developed across the country to address diverse biodiversity questions (Craig 1989).

The effects of possum herbivory on native New Zealand flora were at first usually assessed through aerial photography (Pekelharing 1979) and by helicopter (Pekelharing and Reynolds 1983; Rose *et al.* 1990). However, these methods provided only circumstantial evidence of possum damage, as they could not identify the sources of canopy dieback and defoliation. A more detailed analysis of possum browse could only be made at the individual plant level. Meads (1976) conducted the first such monitoring program in New Zealand between 1969-1974 to estimate the effects of possums on the vegetative growth of rata (see section 1.2.1), but surprisingly few quantitative studies have been conducted since then on other native plant species.

Several studies have used detailed leaf maps to quantitatively assess the leaf area removed from plant individuals by possums (e.g. Coleman *et al.* 1980; Owen 1993), but this method is extremely time consuming and thus, most programmes have instead relied on visual estimates of plant condition or browse levels. Plants are typically given scores according to a categorical ranking system based either on the amount of possum browse or defoliation apparent on the plant or on the density of plant foliage. Meads (1976) and Cowan *et al.* (1997b) then incorporated these two scores in a composite score for overall possum impact (possum impact = [100 X browse score]/ [100 - percent defoliation]). Numerous studies have used visual scoring to estimate the effects of possums on mistletoes (see Chapter 3 for an overview), but many of them have used different scales to categorise browse and foliage density (see Milne 1996 for a review), which has made it difficult to compare studies at different sites and times.

In addition to the visual estimates of browse and defoliation, some mistletoe monitoring programmes have also incorporated additional techniques to assess changes in plant condition. For example, Milne (1996) found that during a three year study in the central North Island, more *Peraxilla tetrapetala* increased in volume within a possum control area than in an area without possum control. Several Department of Conservation offices have also used photomonitoring programmes, where plants are photographed once or twice per year, and the photos are then compared to detect any major changes in plant size or foliage density (Rance 1995; Jones 1997a). Other programmes have adopted a combination of several of these different methods, because it has not been clear which techniques would be most useful in the future (Rance 1995; Milne 1996).

6.2. Methods

In this study, three monitoring methods (leaf maps, visual estimates of browse and foliage density, and photographs) were used to assess the health of the 60 tagged mistletoe plants in the six study populations between February 1997 and February 1998. The experimental design for this study and the methodology for leaf mapping was discussed in section 4.2. Every three months, plant volumes were also calculated using north-south, east-west, and up-down measurements, and visual estimates were made of percent of foliage browsed and percent foliage density on each plant. Percent browse was recorded as the amount of foliage removed by either insects or possums during the

last six months. Foliage density was expressed as a visually estimated percentage of the amount of light blocked by plant foliage, calculated using computer generated images (see Payton *et al.* 1997b).

Plants were also photographed at three-month intervals using Ektachrome slide film on a 35 mm camera with a standard 55 mm lens and a powerful flash (guide number 45, ASA 100, metres). A small wipeboard with a ruler was attached to a plastic, extendable pole, and this sign was held next to the plant while the photo was taken. The ruler provided scale to the photographs and an identification number for each plant and the date could be written on the wipeboard. Photos were always taken from the same set photopoints, defined by the distance (usually 1.5-4.5 metres) and compass bearing to the host trunk. Rather than photographing large plants from far away, two separate pictures were taken of the left and right sides. Plants were usually photographed from between two to four directions to compare results from different angles. *Alepis flavida* plants were not systematically photographed because many plants were intermingled with host branches, making it difficult to distinguish between mistletoe and beech foliage. Nonetheless, several untagged, heavily browsed *A. flavida* at Eglinton and Lake Ohau were photographed for later comparisons. The slides of each plant during different seasons were later visually compared, and the percentage net change in total foliage cover on each plant between February 1997 and February 1998 was estimated.

Linear regressions were used to compare the estimates of change from different monitoring methods. The changes in initial (February 1997) to final (February 1998) volume, percent browse, and percent foliage density were compared to annual leaf flux (both including and excluding branch loss; see below) calculated from leaf maps over all six populations. The visual estimates of change were compared to leaf flux rather than leaf loss because I was interested in the accuracy of the scores in estimating overall change in plant condition rather than leaf loss alone (see section 4.2.3.3 for an explanation of how the change in leaf flux was calculated). However, percent browse was really a measure of leaf loss and was not concerned with new growth per se. Thus, at the population level, comparisons were made between changes in volume, browse, or foliage density and both mean leaf loss and leaf flux (excluding branch loss) for each population over each three-month period. These comparisons were used to determine if any of the three measures accurately reflected leaf loss rather than the net change in leaf area.

Similarly, linear regressions were used to compare estimates of percentage change in foliage according to photographs and changes in volume, percent browse, percent foliage density, and leaf flux (both including and excluding branch loss; see below) according to leaf maps. These comparisons were made between changes from the initial (February 1997) to final (February 1998) values over the four *Peraxilla* populations (the two *A. flavida* populations were not photographed systematically).

For all analyses, changes in volume, browse, and foliage density were expressed as the value at the end of the period divided by the initial value, and these changes were then normalised with a log transformation. Percent foliage change estimated from photographs had a normal distribution without transformation. Total leaf loss was normalised with a square root function. Leaf flux was expressed as the proportion of final to initial leaf number, and these data were normal without transformation. A second leaf flux was also calculated to incorporate branch loss (see section 4.3.1) by using the following formula: total leaf flux= (leaf flux x % of branches still alive in Feb. 1998) + (-1 x % branches lost during the year).

The sample size for each population was 40 (ten plants over four time periods) except for the following exceptions. The Ohau population had one outlier, but regressions with and without this plant produced similar results, so it was included in the results presented. In addition, the two plants that died during the study were excluded from analysis at the appropriate times (see section 4.3.1). Foliage density analyses of one *A. flavida* plant at Eglinton from August-November and November-February were also omitted, because initial foliage density scores equalled zero and the log of zero is undefined.

6.3. Results

6.3.1. Comparing changes in volume, browse and foliage density to leaf maps

Over all six populations, no significant relationship existed between volume, percent browse score, or foliage density score and leaf flux with or without branch loss (Table 6.1). Change in volume was almost significantly related to leaf flux including branch

loss, and change in foliage density was almost related to leaf flux without branch loss. Change in percent browse score showed no trend with leaf flux.

Table 6.1. Linear regressions between the log of changes in volume, percent browse, or percent foliage density and leaf flux or leaf flux plus branch loss for all six populations (n=58; two plants died during the year) between February 1997 and February 1998.

	Change volume (log)	**Change % browse (log)**	**Change % foliage density (log)**
Leaf flux	$R^2 = 0.0339$	$R^2 = 0.0072$	$R^2 = 0.0518$
	$F = 1.97$	$F = 0.41$	$F = 3.06$
	$p = 0.1663$	$p = 0.5260$	$p = 0.0858$
Leaf flux and branch loss	$R^2 = 0.0646$	$R^2 = 0.0003$	$R^2 = 0.0385$
	$F = 3.87$	$F = 0.01$	$F = 2.24$
	$p = 0.0542$	$p = 0.9052$	$p = 0.1401$

At the population level, changes in volume, browse score, and foliage density score did not correspond to leaf area losses measured on the leaf maps in 15 of 18 cases (Table 6.2). Percent browse increased and percent foliage density decreased with increasing percent leaf loss for *Alepis flavida* plants at Eglinton, and a decrease in plant volume was associated with an increase in percent leaf loss on *Peraxilla tetrapetala* at Lake Ohau. In 16 of 18 cases, changes in volume, browse, and foliage density did not significantly correspond to leaf flux (Table 6.3). Increases in foliage density corresponded to more positive net changes in leaf area for *A. flavida* at Eglinton. Unexpectedly, increases in browse score also correlated to more positive annual leaf fluxes for *A. flavida* at Craigieburn. No obvious explanation exists for such a relationship, particularly since browse was not related to leaf loss for this population. No relationship existed between browse and leaf flux for the remaining five populations, and thus, this relationship probably does not signify a more general trend between the two.

Table 6.2. Linear regressions between the square root of average leaf area loss on study plants according to leaf maps and the log of changes in volume, percent browse, and foliage density for each population during each season. Significant results are in bold.

Population	% leaf loss v. change in volume	% leaf loss v. change in % browse	% leaf loss v. change in % foliage density
A. flavida, Craigieburn	$R^2 = 0.0373$ F = 1.47 p = 0.2324	$R^2 = 0.0447$ F = 1.78 p = 0.1903	$R^2 = 0.0034$ F = 0.13 p = 0.7203
A. flavida, Eglinton	$R^2 = 0.1026$ F = 3.66 p = 0.0648	**$R^2 = 0.5418$[b]** **F = 37.84** **p = 0.0000**	**$R^2 = 0.5452$[c]** **F = 38.36** **p = 0.0000**
P. colensoi, Eglinton	$R^2 = 0.0014$ F = 0.05 p = 0.8209	$R^2 = 0.0062$ F = 0.24 p = 0.6298	$R^2 = 0.0117$ F = 0.45 p = 0.5063
P. colensoi, Waipori	$R^2 = 0.0318$ F = 1.12 p = 0.2978	$R^2 = 0.0043$ F = 0.15 p = 0.7040	$R^2 = 0.0084$ F = 0.29 p = 0.5956
P. tetrapetala, Craigieburn	$R^2 = 0.0006$ F = 0.02 p = 0.8801	$R^2 = 0.0000$ F = 0.00 p = 0.9730	$R^2 = 0.0322$ F = 1.27 p = 0.2676
P. tetrapetala, Lake Ohau	**$R^2 = 0.1922$[a]** **F = 9.04** **p = 0.0047**	$R^2 = 0.0043$ F = 0.15 p = 0.7040	$R^2 = 0.0283$ F = 1.10 p = 0.2998

[a] $y = -0.0730x + 0.1323$
[b] $y = 0.0906x - 0.3361$
[c] $y = -0.1799x + 0.8925$

Table 6.3. Linear regressions between annual leaf flux on mapped branches and changes in the log of volume, percent browse, and percent foliage density for each population during each season. Significant results are in bold.

Population	Leaf flux v. change in volume	Leaf flux v. change in % browse	Flux v. change in % foliage density
A. flavida, Craigieburn	$R^2 = 0.0710$ $F = 0.61$ $p = 0.4569$	**$R^2 = 0.4996$[a]** **$F = 7.99$** **$p = 0.0223$**	$R^2 = 0.2905$ $F = 3.27$ $p = 0.1080$
A. flavida, Eglinton	$R^2 = 0.0775$ $F = 0.59$ $p = 0.4682$	$R^2 = 0.3347$ $F = 3.52$ $p = 0.1027$	**$R^2 = 0.4504$[b]** **$F = 5.74$** **$p = 0.0478$**
P. colensoi, Eglinton	$R^2 = 0.1321$ $F = 1.22$ $p = 0.3019$	$R^2 = 0.0205$ $F = 0.17$ $p = 0.6934$	$R^2 = 0.0073$ $F = 0.06$ $p = 0.8139$
P. colensoi, Waipori	$R^2 = 0.1650$ $F = 1.38$ $p = 0.2780$	$R^2 = 0.1675$ $F = 1.41$ $p = 0.2741$	$R^2 = 0.0359$ $F = 0.26$ $p = 0.6255$
P. tetrapetala, Craigieburn	$R^2 = 0.0008$ $F = 0.01$ $p = 0.9365$	$R^2 = 0.0028$ $F = 0.02$ $p = 0.8848$	$R^2 = 0.0672$ $F = 0.58$ $p = 0.4696$
P. tetrapetala, Lake Ohau	$R^2 = 0.0522$ $F = 0.44$ $p = 0.5254$	$R^2 = 0.0054$ $F = 0.04$ $p = 0.8400$	$R^2 = 0.0030$ $F = 0.02$ $p = 0.8804$

[a] $y = 0.4874x + 0.0687$
[b] $y = 2.3990x + 1.6597$

6.3.2. Photographs

6.3.2.1. General observations

Photographs varied widely in their quality and replicability. A powerful flash was essential to "spotlight" the mistletoe plants and to separate them from a dark background. Photographs that were taken in overcast conditions or close to dawn or dusk were easiest to assess for percentage of foliage lost, because the foliage was clearly illuminated by the flash. Bright sunlight made plants appear less healthy because the photos were usually washed out, whereas cloudy weather (and particularly rain) made plants appear more glossy and healthy (Plate 6.1). Plant condition also varied considerably with season. The mistletoes almost always looked most healthy in February after the growth of new foliage, while plants looked most defoliated in September.

In general, the best photos were obtained from small plants that were not more than three metres off the ground and were not intertwined with other foliage. Large plants were more difficult to photograph, and these plants usually had to be photographed in several parts to be exposed properly by the flash. In addition, the *Peraxilla* species were relatively easy to photograph compared to *Alepis flavida*, because the latter species often grows far out on host limbs (Powell and Norton 1994) and can not be distinguished from host foliage. Although the two *A. flavida* study populations were not monitored using photographs, pictures of certain *A. flavida* plants at Craigieburn, Eglinton and Lake Ohau successfully documented cases of severe possum browse (Plate 6.2).

Photopoints, marked by a compass bearing and distance to the host trunk (rather than to the mistletoe itself), ensured that plants were usually replicated well in photographs through time. In some cases, plants were framed vertically in some seasons and horizontally in others, which made it difficult to compare the pictures. In addition, several times photopoints had to be shifted to encompass new growth on the plant or because of fallen debris or the angle of the sun. Most plants were photographed from several angles, and this duplication was useful when one of the photopoints could no longer be used, or when the loss of foliage was apparent from only one vantage point.

Plate 6.1. Photographs of a *P. colensoi* plant (G34) from Eglinton in (**a**) November 1997 and (**b**) February 1998. The foliage appears more dense and healthy during rain (Feb.) than in bright sunlight (Nov.).

a)

b)

Plate 6.2. An *Alepis flavida* plant (B1158) from Eglinton in **(a)** February 1997, **(b)** May 1997, and **(c)** February 1998. The plant was severely possum browsed between Feb. and May 1997, and then produced much new growth by Feb. 1998.

a)

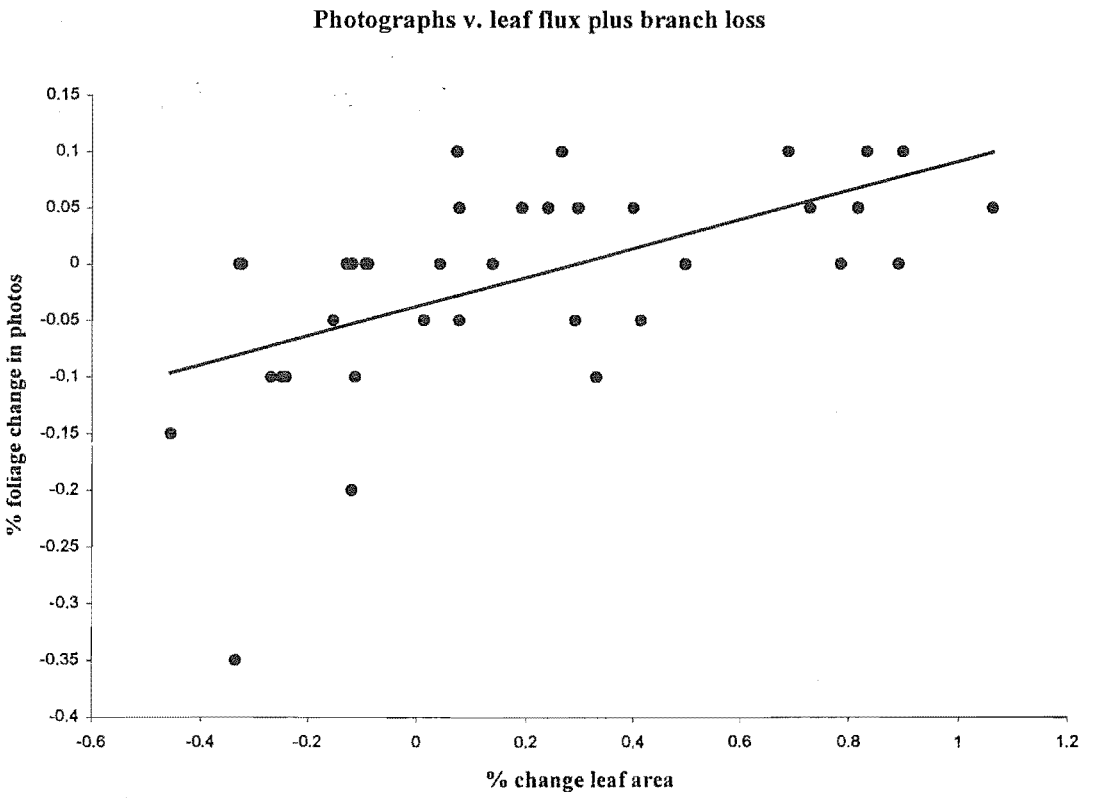
b)

c)

6.3.3.2. Photographs compared to other monitoring methods

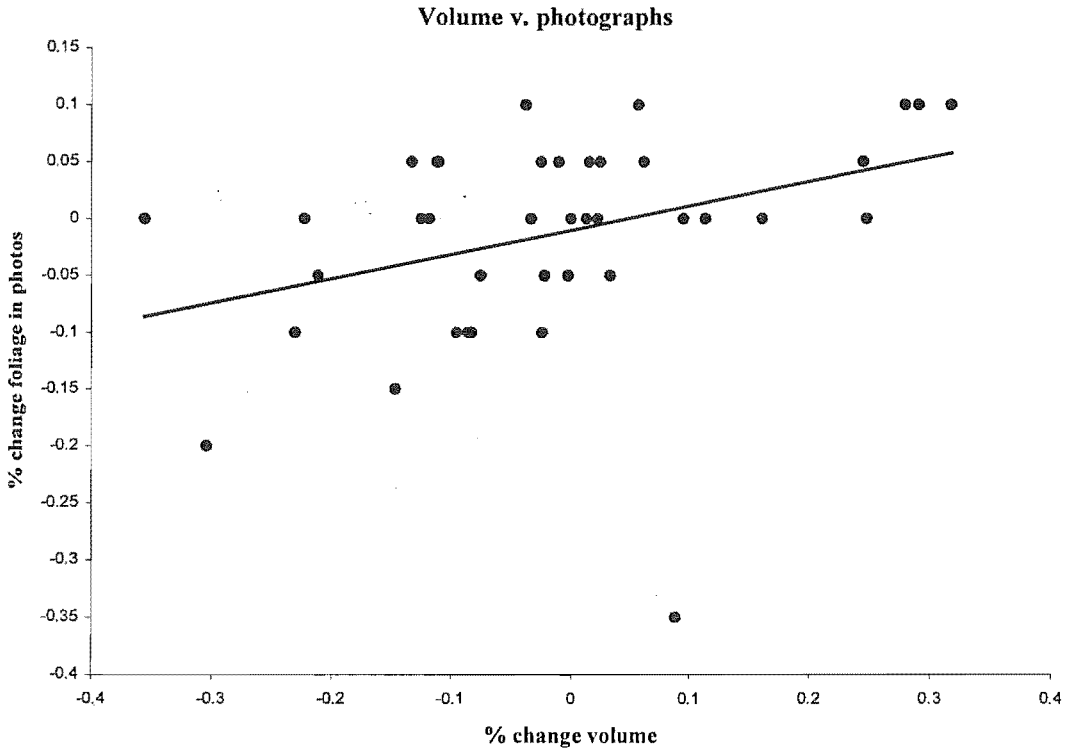
Percent net change in foliage estimated from photographs was not significantly related to leaf flux from leaf maps (R^2=0.05, F=2.10, p=0.1560), but it was strongly correlated with a second measure of leaf flux that included leaf loss on branches that disappeared during the year (Figure 6.1; F=18.45, p=0.0001).

Figure 6.1. Linear regression between percent net change in foliage estimated from photographs and annual leaf flux including branches lost from February 1997-February 1998 in the four *Peraxilla* spp. populations (R^2 = 0.3327, y = 0.1289x - 0.0375).



Annual percent net change in foliage according to photos was not significantly related to annual change in percent browse (R^2=0.04, F=1.64, p=0.2078) or foliage density (R^2=0.03, F=1.28, p=0.2655) for the four *Peraxilla* populations, but it was significantly related to change in plant volume (Figure 6.2; F=5.81, p=0.0210).

Figure 6.2. Linear regression between percent net change in foliage estimated from photographs and change in volume from February 1997-February 1998 in the four *Peraxilla* populations (R^2 = 0.1358, y = 0.2132x - 0.0101).



6.4. Discussion

6.4.1. Comparing monitoring methodologies

6.4.1.1. Leaf maps

Leaf maps provided the most detailed data about leaf loss and the effects of herbivory, and this method is objective and highly replicable across sites and through time. However, leaf maps probably underestimate possum damage, because many browsed leaves abscise and this secondary possum damage is not recorded using this methodology. A correlation between higher than average possum damage and high abscission rates must therefore be used to infer when possums are having a large effect on plants (see section 4.4.1.2). In addition, new growth on plants may be overestimated on leaf maps because all mapped branches include apical tips, where most new growth will occur.

The greatest drawback to leaf maps is that it is extremely labour-intensive and thus, it is simply not a feasible technique for most conservation managers. Also, because it is so time consuming to draw and check the maps, only a small proportion of mistletoe plants in a population (and in turn, only small parts of the chosen plants) can be monitored. These small sample sizes are problematic because possum browse is extremely patchy, and the amount of damage on mapped branches may not accurately reflect the overall damage on a plant or population (see section 4.4.2).

6.4.1.2. Volume measurements

Volume measurements are objective but difficult to replicate, because plants are irregularly shaped and thus must be measured precisely along the same axes every time to produce consistent results. Also, plants are often too high to hold the tape against, which can lead to measurement errors. Moreover, consistent decisions must be made about whether to include certain parts of plants (e.g. protruding branches or dead foliage). If defoliated branches are not eliminated from the volume then defoliation will not be reflected by volume measurements, but if they are excluded and these branches then later produce new leaves, volume measurements will suddenly increase, potentially

exaggerating the increase in plant condition. Another disadvantage of using volume measurements is that the figures are hard to interpret without other detailed information about the causes of defoliation and its effects on plant health.

Although change in volume did not correlate with leaf flux according to leaf maps, the relationship was nearly significant once branch loss was added to the leaf flux equation (Table 6.1). At the population level, change in volume was only significantly related to mean leaf loss on *P. tetrapetala* at Lake Ohau (Tables 6.2 and 6.3). Branch loss is often strongly reflected in volume measurements, and this population and *A. flavida* at Eglinton were the only two populations with significant branch losses (branch loss at Ohau was probably due to wind or snow damage while branch loss at Eglinton was probably caused by possums; see section 4.3.1). No direct measure of branch loss was incorporated into the calculations of mean leaf loss, but branch and total leaf loss may have been correlated at Ohau, because wind may increase both types of damage simultaneously. In contrast, possums heavily defoliated all *A. flavida* plants at Eglinton but broke branches on only some of them, and thus leaf loss was not related to changes in plant size.

These results suggest that volume is a reasonable indicator of overall changes in plant condition, although in many cases, leaf loss and growth may occur without corresponding changes in plant size. These results also highlight the importance of branch loss to overall net change in leaf area on plants. Although branch loss is relatively uncommon (only 6.8% of branches in this study were lost), a large amount of leaf biomass is lost with each branch, and these losses may greatly affect plant health.

6.4.1.3. Percent browse and foliage density scores

Estimates of percent browse and foliage density are the quickest and easiest of the monitoring methods examined, but they are also the least replicable. Scores are subjective and people (and the same person through time) will rate plants differently depending on their current frame of reference (e.g. the architecture of plants varies within and between mistletoe species, plants look different in different weather and during different seasons, flushes of new growth may occur in certain years but not during others). Thus, results may not be comparable over time or across sites. Moreover, architectural differences between plants (e.g. *A. flavida* is more open and less

branched than *Peraxilla* spp., and exposed plants are often more dense than sheltered plants) can influence scores unrelated to differences in plant health. On the other hand, Payton *et al.* (1997b) have developed a monitoring system for a range of native plants using Foliage Cover Index (FCI) scores, which they suggest can be used by two observers to obtain mean FCI scores of only +/-2.5% of each other with 95% confidence.

However, even if browse or foliage density could be consistently scored, this study still suggests that such scores do not correspond to changes in leaf area according to leaf maps, regardless of whether branch losses are included or not (Table 6.1). Percent browse was particularly unrelated to leaf flux, probably because this value reflects only the amount of new browse present and is not concerned with the amount of new growth. In fact, *A. flavida* plants at Craigieburn with more positive leaf fluxes had higher increases in percent browse than plants with more negative leaf fluxes for unknown reasons (Table 6.3). Furthermore, increases in percent browse only corresponded to increases in total leaf loss when plants were severely defoliated (*A. flavida* at Eglinton; Table 6.2).

Change in foliage density scores also did not correlate with leaf flux for the six populations together, although it was a better indicator of leaf flux than percent browse (Table 6.1), since it was an estimate of the overall condition of the plant (including both loss and new growth). Similar to browse scores, foliage scores best corresponded to leaf loss and leaf flux for *A. flavida* plants at Eglinton, which were severely defoliated (Tables 6.2 and 6.3).

Used alone, both browse and foliage density scores may be misleading. Percent browse scores are typically limited to recent (within six months) possum damage. Thus, when plants are severely defoliated and few damage patterns remain on the plant (see section 4.4.1), damagelost through abscission may not be included, and the effects of possums may be underestimated (see section 4.4.1.2). The loss of abscised leaves can only be included when the cause of defoliation can be definitively ascertained. In contrast, foliage density scores estimate overall leaf loss but do not explain the causes of this loss, which could include possums, insects, disease, host damage, wind, or drought. Thus, the overall importance of possum herbivory to plant health can only be assessed by using the two scores together.

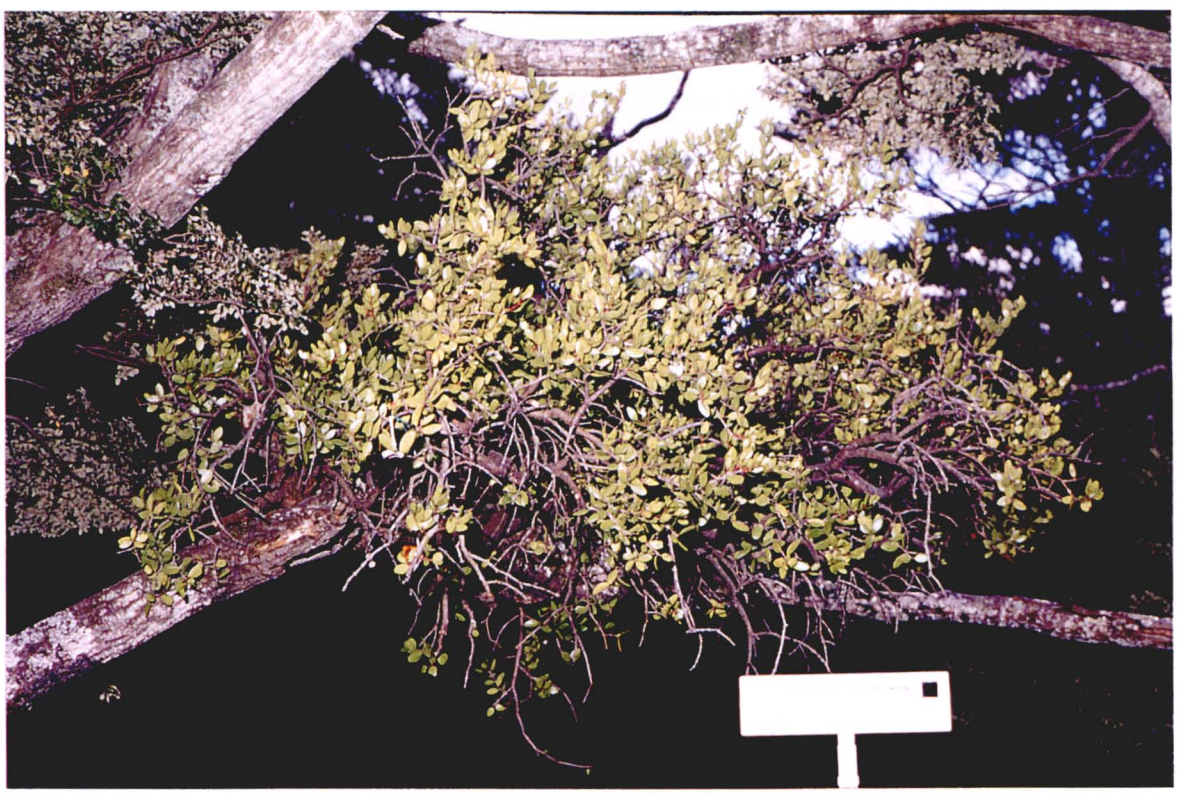
6.4.1.4. Photographs

In contrast to the other methods previously discussed, estimates of percent change in foliage cover taken from photographs corresponded well to leaf flux when lost branches were accounted for (Figure 6.1). These results strongly indicate that photographs are a much better way of estimating changes in plant condition than volume measurements or visual estimates of browse or foliage density. Moreover, branch loss seems to significantly affect overall plant condition in some cases, as discussed above, and photographs may be the only method that can be used to identify when branches disappear (Plate 6.3).

Plate 6.3. A *P. tetrapetala* plant at Lake Ohau (OH52) in (**a**) February 1997 and (**b**) February 1998, before and after losing its bottom branches to wind damage. Annual leaf flux for this plant was +33% when lost branches were not considered but –33% when lost branches were included.

a)

b)



The photograph scores were not significantly related to either changes in percent browse or foliage density scores, but there was a significant relationship with changes in volume (Figure 6.2). This suggests that volume measurements may be the best surrogate for photographs in situations where photomonitoring is not possible. However, although changes in volume corresponded to total leaf flux better than percent browse or foliage density when branch loss was included, foliage density was a better indicator of leaf flux when branch losses were excluded (Table 6.1). Furthermore, at the population level, volume measurements corresponded better to leaf map results on *P. tetrapetala* plants at Lake Ohau, which lost many branches to wind damage but was not affected by possums, while foliage density and browse scores reflected changes in leaf area better on *A. flavida* at Eglinton, which experienced severe possum damage.

Thus, changes in volume may accurately reflect changes in plant condition only when branch loss is the most important factor, while changes in foliage density may accurately represent plant condition only when possums severely defoliate plants. In contrast, photographs can be used to accurately estimate the relative importance of both types of leaf loss. Branch loss was easy to recognise from photographs, and although the most severely possum browsed population, *A. flavida* at Eglinton, was not systematically photomonitored, leaf loss was apparent from photographs of some of these defoliated plants (Plate 6.2).

Photomonitoring has two primary disadvantages. First, the causes of leaf loss are difficult to determine from photos alone, and thus a record of the cause of leaf loss (e.g. a percent browse score) must be made in the field. Second, plants that are located high in host trees or that are intertwined with host foliage (as *Alepis flavida* often is) may be difficult to monitor. Thus, only a subset of the population can be assessed with photographs, although many more plants (and more of each plant) can be monitored than with leaf maps. Although photomonitoring is more expensive and time-consuming to set up than simply using a scoring system, it is relatively simple and fast to re-photograph plants once photopoints are established, and its greater accuracy more than compensates for these relatively minor costs.

6.4.2. Developing national guidelines for mistletoe monitoring

The appropriate methodology for monitoring mistletoes will have to provide the most accurate and detailed information possible while remaining relatively quick and cost-efficient. Clearly, leaf mapping is not a feasible option for most managers, because it would be too time consuming (and thus expensive) to map and frequently re-monitor a sufficient number of plants. On the other hand, a percent browse or foliage density score alone is probably not an accurate assessment of possum damage, even though it is a quick and easy method of monitoring numerous plants.

Photographs correspond closely to changes in leaf area according to leaf maps, but a record of the causes of leaf loss is also needed. Thus, a combination of photomonitoring and scores of percent browse constitutes the most appropriate mistletoe monitoring programme. Photographs provide the best estimate of overall changes in plant condition including branch loss, while browse scores indicate the specific effects of possums. The overall importance of possum browse to plant health can then be assessed by examining the relationship between photographs and browse scores. Volume measurements and foliage density scores are probably not necessary, since leaf loss due to both branch loss and browse is usually apparent from photographs. However, volumes may help to identify plants at later visits, especially when a single host tree supports more than one mistletoe plant.

Milne (1996) highlighted the need for national standards for mistletoe monitoring programmes throughout New Zealand. A set of simple and specific methodological rules should be given to all personnel involved in monitoring to ensure that results are as consistent as possible across the country and through time. Appendix 2 outlines a suggested monitoring protocol developed from the results of this study.

6.4.3. The importance of scale

Norton (1996) recognised that any monitoring program must be attentive to the scale at which the processes of interest operate. Scale is particularly important to programs assessing possum damage on mistletoes, because these effects are so heterogeneous in both space and time (see section 4.4.2). Possums appear to browse only a small subset of mistletoe individuals within a population, and therefore, enough plants must be monitored to ensure that some of these browsed individuals are recorded. A large

sample size is thus crucial to any mistletoe monitoring program, even though this will increase the time and money required.

Mistletoe monitoring also needs to be attentive to the temporal patchiness of possum browse as well as the rates of turn-over and the life-cycles of the mistletoes themselves. Possums may damage plants suddenly and severely within a short time, and the obvious effects of browse may disappear quickly once new leaves have sprouted (personal observation). Thus, plants must be monitored frequently enough to accurately describe these attacks. Also, plant appearance and the relative palatability of plants to possums may change seasonally (Ogle and Wilson 1985). Milne (1996) suggested that mistletoes be monitored in the summer when fruiting and flowering can be recorded, but Norton (1997) pointed out that spring flushes of new growth can lead to overestimates of plant health. Thus, ideally plants should be monitored twice each year: during the winter when plants appear at their worst, plants should be photographed and given a browse score, and during the summer, a quick revisit can be conducted to evaluate browse scores again and to record fruiting and flowering. This also allows seasonal shifts or sudden changes in possum diet to be recorded (e.g. Owen and Norton 1995), and assessing the cause of leaf loss will be easier because browse will never be more than six months old before it is recorded.

Perhaps the most important aspect of temporal scale for mistletoe monitoring is that possum effects on plant health may only be recognisable over relatively long time periods. Milne (1996) estimated that plants could take at least five years to recover from possum browse, and the effects on reproduction may be even longer term. Results from the Hurunui and Eglinton Valley Department of Conservation monitoring programmes also suggest that defoliation may be sudden, while regrowth probably occurs more gradually (see section 3.3). Population level effects will also be difficult to detect except through long-term studies, because mistletoes are slow growing plants with a low reproductive rate. Furthermore, the effects of possums at any site may change rapidly without corresponding increases in local possum densities. For example, plants at Waipori were heavily attacked prior to December 1996 but remained stable over the entire subsequent year in the absence of any possum control. Moreover, mistletoe plants in the Moeraki area on the West Coast of the South Island have declined over a three year period even where possum control was conducted (Overmars 1997a). Without long-term data, it is impossible to determine whether such changes

indicate long-term trends or shorter term changes within a highly fluctuating system, and what the overall consequences of this damage will be for mistletoe individuals and populations.

6.5. Conclusions

A comparison of three monitoring methods has indicated that the most appropriate programme will include photographing mistletoe plants each winter and visually estimating a percent browse score twice per year, during the winter and summer. A large number of plants (at least 30 per site, depending on their local abundance) should be monitored for a long time period. Specific guidelines for such a programme are provided in Appendix 2. Unfortunately, this mistletoe monitoring programme will require considerable resources, but less rigorous methodologies may not only yield insufficient information but even produce misleading results that could lead to inappropriate management decisions.

At the beginning of this chapter, I listed five key goals of past mistletoe monitoring programmes:

1. to assess changes in mistletoe health;
2. to assess the impact of possums on mistletoe health;
3. to assess the effectiveness of possum control operations;
4. to assess changes in plant communities since possum colonisation; and
5. to assess the overall impact of possums on entire beech forest communities.

The methodology that has been proposed based on the results of this study was chosen specifically as the best way to accomplish the first two goals of assessing changes in mistletoe health and determining whether or not possums are responsible for any observed declines. However, this programme can only assess the "effectiveness" of possum control operations if success is defined as increases in mistletoe health and if the area is monitored both before and after the control operation (or alternatively, in adjacent areas with and without control). The effects of possum control on other native species in that ecosystem cannot be predicted based on changes in mistletoe health, because possums selectively feed on certain plant species independent of the local density of those species. In addition, certain plants may be preferred over mistletoes by possums or have shorter adult longevity, both of which could cause these species to

decline more rapidly than mistletoe populations. Thus, the final two goals, which use mistletoes as an indicator for more general changes in the local community, also cannot be achieved through mistletoe monitoring programmes. Monitoring should be conducted to assess changes in mistletoe health alone, although possum control operations are likely to benefit other native species, and improvements in mistletoe health will also directly benefit native birds such as the bellbird and tui.

CHAPTER 7: CONCLUSIONS

The main purpose of this study was to ascertain the overall importance of possum herbivory to native beech mistletoes relative to insect herbivory and other sources of leaf loss. Although numerous anecdotal reports have suggested that possums severely damage mistletoes (Ogle and Wilson 1985; Ogle 1997), the only two quantitative studies of possum effects have presented contradictory evidence. Wilson (1984) found that the three beech mistletoe species at Mt. Misery declined in condition because of possum browse (although the causal link between possum damage and mistletoe decline was not proven), whereas Owen (1993) found that possums contributed little to overall leaf loss on *Peraxilla colensoi* in the Upper Haast Valley. Furthermore, mistletoes have declined in some areas not inhabited by possums (Ogle and Wilson 1985; Ogle 1997), and mistletoes and possums co-exist at sites such as Craigieburn.

Results from this study suggest that variation in possum damage to mistletoes does exist at a number of scales, but also that the monitoring methods used in the past have not always accurately estimated damage levels across mistletoe populations. Both factors have probably heightened debate over the relative importance of possums to overall mistletoe decline. Although this study offers no definitive answer to this debate, it does suggest that patterns of variation in possum browse at various spatial and temporal scales have crucial implications both for plant health and for the way in which we monitor mistletoes.

7.1. IMPORTANCE OF HETEROGENEITY

In Chapter 4, I presented leaf map data that showed that at the population level, both possums and insects caused only a small proportion of total leaf loss on the 60 plants in the six study populations. Annual losses from insects and possums in all but two cases were less than 3% of total leaf area. In the remaining two cases, *Peraxilla colensoi* at Eglinton had a similar level of insect damage (8.57%) as *Alepis flavida* at Eglinton had from possums (7.05%), but extremely high abscission rates were only associated with

the possum damage on *A. flavida*, not the insect damage on *P. colensoi*. This association suggests that unusually high levels of abscission may be secondary possum damage, and observations indicated that possums were responsible for the almost complete defoliation of the Eglinton population in less than six months.

Thus, this study verifies previous reports that possum browse is more variable and can be much more severe than insect browse. A lot of emphasis has been placed on these regional differences, and numerous studies have found that possum dietary preferences shift across sites independent of local plant availability (e.g. Mason 1958; Fitzgerald 1976; Leathwick *et al.* 1983; Green 1984; Coleman *et al.* 1985). Other studies have also shown remarkable variation in browse on plant individuals within a population (e.g. Meads 1976; Owen 1993), but the potential implications of this patchiness for the long-term persistence of plant populations has been largely overlooked. This study indicates that the heterogeneity of possum browse at these various scales can have important effects on the health of mistletoe populations.

Although possums and insects removed similar amounts of biomass at the population level, possum browse varied between plants much more than insect browse. While all plants were damaged by insects during most of the year, only 32% of plants lost any leaves to possums. Thus, insect browse was probably a relatively predictable stress for mistletoes, whereas possum browse was unpredictable because it was concentrated on a small number of plants, often during a short time period. Furthermore, browsed plants in this study lost more leaves than they could produce over the year, whereas unbrowsed plants experienced a net increase in leaf area. This difference indicates that possum browse may induce mortality, particularly since plants are frequently re-browsed. Thus, possums could potentially cause the slow population-level decline of plants such as mistletoes with long life-spans and slow growth, because the deaths of a few heavily defoliated individuals could increase the mortality rate above the recruitment rate (Table 7.1).

Table 7.1. Summary of the effects of insects versus possums over all sites and species of mistletoe plants in this study from February 1997 to February 1998.

	Insects	**Possums**
Leaf loss (% total area)	2.77	1.82
Heterogeneity between plants (c.v.)	1.17	2.74
Plants damaged (%)	100	32
Maximum severity (max. 3-month % leaf loss on a plant)	8.9	26.9 (100 including loss via abscission)
Predictability	high	low
Deaths	unlikely, unless epidemic	few
Population-level effect	none?	decrease over time?

In Chapter 5, I examined some of the potential causes of this heterogeneity in possum damage. Patchiness within individual plants was related to leaf age, and possibly to the location of branches on a plant. Variations in browse between plant individuals in each population did not predictably depend on plant height, location within the forest (edge or interior), or palatability. However, sample sizes were small and more detailed investigations are needed before ruling out these potential effects. Browse between plants was related to plant volume for *P. colensoi* (larger plants lost a greater proportion of their leaves than smaller plants), which could also reflect plant age. Plant shape, proximity to den sites, exposure, and accessibility to possums are additional factors that could influence possum activity but that were not investigated in this study.

7.2. Monitoring Techniques

The heterogeneity discussed above means that mistletoe monitoring programs must be developed cautiously in order to avoid misinterpretation of this variation as overall trends in population health. Therefore, the most important consideration for conservation managers may be to ensure that large sample sizes are monitored at relatively frequent intervals (at least annually) for long time periods. Drastic changes in plant health may be relatively easy to detect, but low levels of mortality will be less obvious--although no less important--to long-term population persistence. Thus, monitoring methods need to be as consistent and objective as possible to enable comparisons through time and across the country. In Appendix 2, I recommend a

standard methodology that includes photomonitoring and visual estimates of possum browse.

Mistletoes have been used as "flagship species" for conservation efforts in some regions (Walls 1997), because they are considered highly palatable (and vulnerable) to possums and managers assume that other species will benefit from possum control in a similar manner to mistletoes. While this may be a practical way of garnering public support and funding for possum control, managers must remain aware that the only appropriate goal for mistletoe monitoring programs is to monitor the health of a specific mistletoe population. The data presented suggest that possum densities are not predictable based on amounts of damage on mistletoes. Furthermore, possums do not threaten any structural component of beech forests (Wardle 1984), and thus changes in mistletoe health do not indicate similar changes in ecosystem properties or processes (O'Donnell 1995), except possibly if the decline of mistletoes influences native bird densities. Most importantly, mistletoe health cannot be used to predict when possums might be a hazard to other native species, because all species are not equally vulnerable to possum damage (O'Donnell 1995). In fact, mistletoes may be poor indicators because: 1) they might not be strict "ice cream" plants (i.e. often other plants may be preferred), and 2) their long life span and low reproductive rate makes damage difficult to recognise before it is well advanced.

7.3. Future work

This study has indicated that the following three subjects require further investigation:

1. *Effect of possums on mistletoe reproductive output:* Possums are known to ingest the flowers and fruits of beech mistletoes (Wilson 1984; Owen 1993; personal observations), but the extent of this damage and its effects on recruitment have not been studied. The direct loss of fruits and flowers is more costly to plants than the equivalent leaf loss in terms of energetics, because reproductive parts require more resources to produce than vegetative parts. In addition, possum herbivory could lead to an indirect decline in reproductive output, because damage to vegetative parts causes plants to invest less in flowering the following season. The loss of flowers and fruits also has implications for native bird pollinators and dispersers, as well as for insects that feed on the mistletoe flowers (e.g. *Zelleria* spp.).

2. *Relative palatability of mistletoes:* More detailed studies of mistletoe palatability are needed to determine if *Alepis flavida* is preferred to *Peraxilla* spp. in different regions, and to what degree *Peraxilla* spp. and *Nothofagus* spp. actually differ in palatability. This study did not indicate regional differences in palatability between *P. tetrapetala* at two sites, but a larger study would be useful to extend these findings. Variations in palatability between plants in a population also need further investigation, because small chemical differences may determine possum preferences (Lawler *et al.* 1998). If chemical differences do exist, it will be important to determine whether they are environmentally or genetically controlled in order to predict future patterns of damage. Field tests could also help to determine whether possums re-browse certain individuals because of an induced chemical change in leaves after browse (as for rata; Payton 1989).

3. Mistletoe recovery: This study indicates that browsed plants can recover if they are protected from browse, because browsed and unbrowsed plants only differed in the amount of leaf area lost but not in the amount of new leaves produced. However, the interval that mistletoes require for recovery is not known. Mistletoes have shown a variety of responses to release from browse, and while some populations have appeared to benefit quickly from possum control operations (e.g. Hurunui), other populations have required longer to recover (e.g. Eglinton). More data are necessary to estimate how long and to what degree possum control must be maintained to protect mistletoes. For example, would pulses of control resulting in intervals of relatively low possum density enable plants to survive? Low residual possum populations have retarded the recovery of other plant species (Payton *et al.* 1997a) and may similarly affect mistletoes.

The three beech mistletoe species may also have different recovery rates, since *P. tetrapetala* (and probably *P. colensoi*) have the capacity for reiteration, which may enable these species to recover more rapidly than *A. flavida* (Powell and Norton 1994). Finally, the consequences of repeated browsing should be studied, as well as how the timing of browse changes the consequences for plant growth and survival. Heavy defoliation of new growth over spring and summer could particularly harm mistletoe plants, since only one flush of new growth is produced each year.

7.4. CONCLUDING REMARKS

Over the past few years, there has been a surge of interest in native mistletoes in New Zealand, and in particular, how possum control may benefit these increasingly rare species. As a result, the effects of possums in beech forest have become apparent, and numerous monitoring programmes have been established, often in conjunction with possum control operations. Unfortunately, these programmes were developed in the absence of national guidelines to ensure consistency among studies, and thus, the results from various sites have been difficult to compare and no evidence has been collected to endorse one methodology over the others.

This study provides the first quantitative comparison of monitoring methods, and the results show that certain characteristics of possum browse (i.e. patchy, unpredictable, but often locally severe damage) mean that visual scoring methods are less accurate than photographs. Clearly, conservation managers have restrictions on the amount of money and time they can afford for any single conservation project, but a small increase in input (i.e. for photographs, or to monitor more plants) is well worth the effort for more accurate information on which to base management decisions. Programmes will have to be individually tailored to suit the local situation, but adherence to certain guidelines will facilitate comparisons at a national scale and thereby add to our understanding of the ecology and conservation of these important and unique native species. The results of this study also emphasise that mistletoe monitoring programmes must have clearly defined aims, preferably focused on mistletoe health rather than using mistletoes as indicators for other aspects of the ecosystem. Mistletoes are important ecosystem components (as nectar and fruit sources for birds), but this thesis shows that they are not necessarily the most palatable (and hence most at risk) plant species in all beech forest habitats.

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APPENDICES

APPENDIX 1: ADDITIONAL STATISTICS FOR GLM ANALYSES

Table A1: Analysis of variance with leaf flux as the response and the following predictors: 1) plant browsed or unbrowsed ("browse"), 2) site, 3) species, 4) interactions between browse and species, and 5) interaction between browse and site. (Refer to Table 4.8).

Model	**Df**	**Sum of Squares**	**Mean Square**	**F-value**	**Pr(F)**
Browse	1	1.46	1.46	13.60	0.0006
Site	3	3.14	1.05	9.73	0.0000
Species	2	3.41	1.71	15.86	0.0000
Browse: Species	2	0.04	0.02	0.17	0.8447
Browse: Site	2	0.13	0.07	0.61	0.5487
Residuals	49	5.28	0.11		

Table A2: Analysis of variance test conducted for each population with percent leaf loss from abscission (square root) as the response and season, plant location, and the interaction between season and location as predictors. Plant location was not used as a predictor for *A. flavida* at Eglinton because all plants were located along the forest edge. (Refer to tables 5.9 and 5.10).

Species/site	Model	Df	Sum of squares	Mean square	F-value	Pr(F)
A. flavida,	season	1	44.40	44.40	35.53	0.0000
Craigieburn	plt location	1	0.61	0.61	0.49	0.4888
	season: location	1	0.02	0.02	0.01	0.9070
	Residuals	36	44.99	1.25		
A. flavida,	season	1	95.87	95.87	12.62	0.0011
Eglinton	Residuals	34	258.29	7.60		
P. colensoi,	season	1	0.20	0.20	0.16	0.6921
Eglinton	plt location	1	1.77	1.77	1.38	0.2474
	season: location	1	0.00	0.00	0.00	0.9690
	Residuals	36	46.06	1.28		
P. colensoi,	season	1	0.02	0.02	0.03	0.8738
Waipori	plt location	1	1.25	1.25	1.30	0.2622
	season: location	1	0.02	0.02	0.03	0.8747
	Residuals	36	34.72	0.96		
P. tetrapetala,	season	1	2.03	2.03	6.71	0.0137
Craigieburn	plt location	1	0.26	0.26	0.87	0.3564
	season: location	1	0.33	0.33	1.10	0.3011
	Residuals	36	10.88	0.30		
P. tetrapetala,	season	1	6.89	6.89	6.57	0.0147
Ohau	plt location	1	0.55	0.55	0.52	0.4736
	season: location	1	0.46	0.46	0.44	0.5099
	Residuals	36	37.76	1.05		

Table A3: a) Analysis of variance tests conducted for the three populations where insect damage could be normalised with a square root function, and b) binomial GLM's for the three populations which had insect damage that could not be normalised. In both cases, percent leaf loss from insects was the response and season, plant location, and the interaction between season and location were predictors. Plant location was not used as a predictor for *A. flavida* at Eglinton because all plants were located along the forest edge. (Refer to Tables 5.11 and 5.12).

a) Analysis of co-variance

Species/site	Model	Df	Sum of Squares	Mean square	F-value	Pr(F)
P. colensoi, Eglinton	season	1	0.01	0.01	0.03	0.8643
	plant location	1	0.92	0.92	2.32	0.1368
	season: location	1	0.70	0.70	1.77	0.1918
	Residuals	36	14.28	0.40		
P. colensoi, Waipori	season	1	1.67	1.67	7.68	0.0088
	plant location	1	0.25	0.25	1.17	0.2874
	season: location	1	0.48	0.48	2.19	0.1480
	Residuals	36	7.83	0.22		
P. tetrapetala, Ohau	season	1	0.00	0.00	0.02	0.8878
	plant location	1	0.06	0.06	0.42	0.5235
	season: location	1	0.04	0.04	0.24	0.6292
	Residuals	36	5.44	0.15		

b) Binomial

Species/site	Model	Df	Deviance	Residual Df	Residual Deviance	Pr(Chi)
A. flavida, Craigieburn	null			39	42.65	
	season	1	2.39	38	40.26	0.1221
	plant location	1	0.15	37	40.11	0.6960
	season: location	1	0.49	36	39.62	0.4838
A. flavida, Eglinton	null			35	49.80	
	season	1	5.23	34	44.57	0.0222
P. tetrapetala, Craigieburn	null			39	55.35	
	season	1	19.61	38	35.74	0.0000
	plant location	1	4.71	37	31.03	0.0300
	season: location	1	1.79	36	29.24	0.1807

Table A4: Binomial GLM's for the five populations which had possum damage during the year. Percent leaf loss from possums was the response and season, plant location, and the interaction between season and location were predictors. Plant location was not used as a predictor for *A. flavida* at Eglinton because all plants were located along the forest edge. (Refer to Tables 5.13 and 5.14).

Species/site	Model	Df	Deviance	Residual Df	Residual Deviance	Pr(Chi)
A. flavida,	null			39	30.14	
Craigieburn	season	1	0.05	38	30.10	0.8306
	plant location	1	7.66	37	22.44	0.0057
	season: location	1	0.00	36	22.44	0.9992
A. flavida,	null			35	40.49	
Eglinton	season	1	12.62	34	27.87	0.0004
P. colensoi,	null			39	33.82	
Eglinton	season	1	0.63	38	33.18	0.4257
	plant location	1	1.39	37	31.79	0.2387
	season: location	1	0.00	36	31.79	0.9969
P. colensoi,	null			39	33.82	
Waipori	season	1	0.00	38	33.82	1.0000
	plant location	1	6.82	37	26.99	0.0090
	season: location	1	0.00	36	26.99	0.9999
P.	null			39	15.88	
tetrapetala,	season	1	0.00	38	15.88	0.9999
Craigieburn	plant location	1	0.37	37	15.51	0.5436
	season: location	1	5.95	36	9.56	0.0147

Table A5: An analysis of variance test was conducted for each population with the percent total leaf loss (square root) as the response and the following predictors: 1) plant height, 2) season, 3) plant volume, 4) interaction between plant height and season, 5) interaction between volume and season, 6) interaction between volume and height, and 7) interaction between volume, height, and season. (Refer to section 5.4.2.5).

Species/site	Model	Df	Sum of squares	Mean square	F-value	Pr(F)
A. flavida, Craigieburn	height	1	3.14	3.14	2.69	0.1105
	season	1	39.30	39.30	33.77	0.0000
	volume	1	0.69	0.69	0.59	0.4483
	height: season	1	0.52	0.52	0.45	0.5069
	volume: season	1	0.01	0.01	0.00	0.9473
	volume: height	1	0.68	0.68	0.58	0.4507
	vol: ht: season	1	3.20	3.20	2.75	0.1068
	Residuals	32	37.24	1.16		
A. flavida, Eglinton	height	1	1.21	1.21	0.16	0.6961
	season	1	106.57	106.57	13.69	0.0009
	volume	1	9.87	9.87	1.27	0.2697
	height: season	1	3.30	3.30	0.42	0.5204
	volume: season	1	5.67	5.67	0.73	0.4006
	volume: height	1	1.42	1.42	0.18	0.6721
	vol: ht: season	1	0.39	0.39	0.05	0.8243
	Residuals	28	218.02	7.79		
P. colensoi, Eglinton	height	1	0.45	0.45	0.31	0.5817
	season	1	0.06	0.06	0.04	0.8359
	volume	1	7.77	7.77	5.39	0.0267
	height: season	1	0.03	0.03	0.02	0.8883
	volume: season	1	0.22	0.22	0.15	0.6997
	volume: height	1	0.35	0.35	0.25	0.6239
	vol: ht: season	1	0.85	0.85	0.59	0.4474
	Residuals	32	46.08	1.44		
P. colensoi, Waipori	height	1	2.16	2.16	2.99	0.0950
	season	1	1.18	1.18	1.64	0.2108
	volume	1	1.05	1.05	1.46	0.2373
	height: season	1	0.00	0.00	0.00	0.9521
	volume: season	1	4.72	4.72	6.54	0.0163
	volume: height	1	0.90	0.90	1.24	0.2749
	vol: ht: season	1	2.26	2.26	3.14	0.0874
	Residuals	28	20.21	0.72		
P. tetrapetala, Craigieburn	height	1	0.01	0.01	0.02	0.8824
	season	1	4.38	4.38	11.58	0.0018
	volume	1	0.42	0.42	1.12	0.2983
	height: season	1	0.88	0.88	2.31	0.1380
	volume: season	1	0.24	0.24	0.64	0.4306
	volume: height	1	0.39	0.39	1.02	0.3201
	vol: ht: season	1	0.02	0.02	0.05	0.8193
	Residuals	32	12.12	0.38		
P. tetrapetala, Ohau	height	1	0.43	0.43	0.47	0.4961
	season	1	5.80	5.80	6.43	0.0163
	volume	1	0.03	0.03	0.03	0.8621
	height: season	1	1.15	1.15	1.27	0.2679
	volume: season	1	0.86	0.86	0.96	0.3354
	volume: height	1	0.46	0.46	0.51	0.4825
	vol: ht: season	1	1.59	1.59	1.76	0.1935
	Residuals	32	28.85	0.90		

APPENDIX 2: GUIDELINES FOR MISTLETOE MONITORING PROGRAMMES

A. Programme design

1. Mistletoes may be monitored with transect lines, plots, or if plants are rare, using as many individuals as can be located. If transect lines are used, short lines (approximately 20 m long) should be laid out across the study area to ensure a large, independent sample size. Ideally, ten lines should be placed at least 100 m apart, but the number of lines and spacing may need to be adjusted depending on the density of mistletoes and the overall size of the area of interest. If plots are used instead, ten 10 m x 10 m plots should be spaced across the site at 100 m intervals (again the number of plots and spacing will vary from site to site). Either the lines or the plots (not the plants) are individual samples, and thus, all mistletoe plants encountered should be permanently tagged and monitored, because possums may browse one plant and leave adjacent ones alone for no obvious reason. If mistletoes are locally uncommon or the study area is small, lines or plots may not be feasible and plants must be tagged where available. In this case, it is important that as many plants as possible are monitored (at least 50 plants is preferable).
2. Plants should be monitored twice per year in February and August. During the winter, mistletoes should be photographed and given a percent browse score, and in the summer, plants can be quickly given a percent browse score and flowering and fruiting levels can be recorded. Even if not all plants can be photographed (e.g. in mature silver beech forest, where most mistletoes are located high in their hosts), an attempt should be made to photograph at least a subset of the plants. (This may mean that easily visible mistletoes will have to be sought out, even outside of the study transects or plots).
3. Monitoring should continue for at least five years, even if no possum damage is recorded during the first few years. Possums may change their browsing habits and severely affect a mistletoe population within a short time period. Even if plants are not attacked, valuable baseline data on the growth and mortality of unbrowsed plants will be collected.

B. Photographs

1. Slides of plants should be taken using a powerful flash (guide number ≥45, ASA 100, metres) and a 55 mm lens. A pole with a sign should be used to identify the plant and date and to provide scale (the pole can be rested on the host tree if only one person is conducting the monitoring). Prints may be produced from the slides to assist in relocating plants at later times.
2. Photographs should always be taken from photopoints that can be marked permanently with a metal stake. The bearing and distance to the host trunk should always be noted so that the photopoint can be relocated if the marker is removed.
3. Photopoints should be far enough away from the mistletoe to allow for the addition of new growth but close enough to allow the flash to illuminate the plant (large plants may need to be photographed in sections). A distance of about 1.5- 4.5 m from the host trunk is recommended.
4. Whenever possible, plants should be photographed from several photopoints to detect damage on distinct sides of a plant or in case the sun or fallen debris precludes later photographs from one of the points.
5. Photographs should be taken using a consistent frame orientation (vertical or horizontal). Weather can significantly affect the appearance of plants in the photographs, so monitoring should be conducted at dawn or dusk or during an overcast (but not rainy) day.
6. Photographs should be compared each year to previous photos, and the percent change in foliage cover over the past year should be estimated for each plant. Computer generated images can be used to calibrate subjective estimates of changes in foliage cover (see Milne 1996).

C. Percent browse scores

1. Twice per year, each plant should be given a visual estimate of the percent of total foliage that appears to have been removed by possums during the previous six months (i.e. since the last monitoring check). Insect damage should not be included, and abscised leaves should only be included when defoliation was clearly caused by possums (e.g. petioles and torn twigs on the ground or obvious possum damage on neighbouring mistletoe plants).
2. The percent browse score can be compared to percent foliage loss according to photographs using a linear regression. A significant correlation indicates that

possums are affecting plant health. If there is no correlation, declines in plant condition are probably due to some other factor.

D. Other considerations

1. Plants that die during the study do not need to be re-photographed, but they should continue to be checked every year, because apparently dead plants can eventually resprout new leaves (C. Rance and P.R. Wilson personal communication).
2. Mistletoes (especially *P. tetrapetala*) often grow in distinct clumps and may or may not maintain haustorial connections between these clumps (Powell and Norton 1994). These clumps have at least some physiological autonomy and may differ in overall condition. It is easiest to monitor distinct clumps as separate individuals, but it must be possible to distinguish the individuals at later times. Volume measurements, height off the ground, and photographs can all be useful in subsequently identifying plants, particularly when numerous individuals occupy a single host tree.
3. Detailed field notes are an important part of this monitoring programme. Information about environmental conditions, the health of non-monitored plants and species in the area, and other details about the monitored plants may all be useful in interpreting monitoring data.